# The life history and ecology of the aberrant bathypelagic genus *Benthomisophria* Sars, 1909 (Copepoda: Misophrioida)

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## Introduction

The copepod order Misophrioida comprises the littoral genus *Misophria* Boeck, 1864 and the rare bathypelagic genus *Benthomisophria* Sars, 1909. The only published records of the latter genus are those of Sars (1909), Hulsemann & Grice (1964) and Tanaka (1966 – as *Misophria*). Little is known of the life history and ecology of either of the two *Benthomisophria* species, primarily because of the difficulty in obtaining large samples of these bathypelagic forms. In 1976 the Institute of Oceanographic Sciences commenced a total water column sampling programme, integrating midwater, near-bottom and benthic hauls. A new technique for taking near-bottom samples was employed and this is described in detail below. Analysis of the first complete series taken under this programme revealed large numbers of *Benthomisophria,* including many developmental stages. These specimens were found to belong to *B. palliata* Sars, 1909 and to *B. cornuta* Hulsemann & Grice, 1964. The 5 copepodid stages of *B. palliata,* 3 copepodid stages and male of *B. cornuta* are described for the first time. Notes on the vertical distribution of both species are presented, and phylogenetic relationships within the Misophrioida are examined.

## Materials and methods

### Sampling methods

The samples were taken with the acoustically controlled RMT 1+8 net system described in Baker, Clarke & Harris (1973). The small mouth area RMT 1 has a mesh size of 320 μm and the larger RMT 8 has a 4·5 mm mesh. The effective mouth areas of these nets vary with towing speed (Baker *et al.,* 1973; Roe & Baker, in prep.). The nets are opened and closed acoustically using a telemetering net monitor that activates a mechanical release gear. The monitor continuously telemeters the depth, temperature, speed and distance travelled (collectively called flow) and an indication of whether the nets are open or closed. This information is displayed on the ship on a modified Mufax facsimile recorder (Roe & Harris, in press).

The sampling programme required samples to be taken in discrete depth layers from just above the sea bottom to the surface. In order to fish the nets to within approximately 5m of the sea bed in depths of 4000m a system of bottom indicator switches was used. This consisted of 2 mercury switches, each encased in a streamlined protective housing, connected to the net monitor by a single protected conducting cable. The cable was fixed down the side wires of the nets to the weight bar, and the switches hung below this bar so that their estimated distances below the bottom bar when fishing were 5m and 20m respectively. The near-bottom hauls were made by paying out the net until it was within 20m of the bottom, as shown by the lower indicator switch hitting the sea bed and tilting so that the mercury within the switch made an electrical contact. This contact was telemetered back to the ship where it was displayed on the Mufax as a displacement of the net indicator trace. Paying out more warp caused the second switch to hit the sea bed, resulting in a further displacement of the net trace. The first shift in this trace therefore indicated that the net was about 20m above the sea bed and the second that it was about 5m above the bottom.

The net was then opened and maintained within this 5–20m layer by adjusting the amount of warp so that the 20m indicator was continuously registering with the 5m indicator appearing intermittently. Two hauls, Station numbers 9541 # 18 and 19 (Table 1), were made in this way. The remaining hauls sampled progressively further from the bottom.

**Table 1** Station data of the hauls in which *Benthomisophria* spp. were found.

| Station No. | Sounding range (m) | Mean Sounding (m) | Depth off bottom of sample (m) | Depth from surface of sample (m) | Duration of haul (H) |
|---|---|---|---|---|---|
| 9541# 18 | 3974–4036 | 4005 | 5–20 | | 6 |
| #19 | 4008–4060 | 4031 | 5–20 | | 6 |
| #22 | 3856–3914 | 3883 | 20–100 | | 6 |
| #24 | 4000–4079 | 4035 | 100–500 | | 6 |
| #25 | 4008–4105 | 4058 | 500–1000 | | 6 |
| | Σ3856–4105 | 4002 | | | |
| #26 | 3918–3945 | 3934 | | 2510–3000 | 4 |
| #27 | 3839–3889 | 3860 | | 2000–2500 | 4 |
| 9131# 18 | 3870–3896 | 3884 | 20–100 | | 4 |
| #19 | 3957–4036 | 3998 | 100–500 | | 5 |
| #23 | 3865–3934 | 3905 | 500–1000 | | 4 |

Since the net was a considerable distance behind the ship during these deep hauls the bottom depth over which it was actually fishing was derived as follows. The sounding beneath the ship was recorded on a Precision Echo Sounder (PES) continuously during the paying out and retrieval of the nets and periodically throughout the fishing periods. From these data a bathymetric chart of the area was subsequently constructed. The bottom was found to be essentially flat with the soundings in each haul varying by less than 100m (Table 1) in a total distance travelled over the ground of between 19·1–21·9 Km. The position of the net whilst fishing was calculated by triangulation – knowing at a given moment the ship's course, the depth below the ship and the amount of wire out. Because the gradient of the bottom was so slight it was possible to ignore errors in triangulating the net position caused by a changing depth and by lateral displacement of the net behind the ship. This calculated net track was then superimposed upon the bathymetric chart and the mean bottom depth over which the net had fished was derived from the soundings taken at every one minute of longitude on the chart.

Station number 9541 # 22 (Table 1) fished between about 20 and 100m off the bottom. The 20m indicator switch was used to determine the lower limit of the haul whereas the upper limit was obtained from the monitor depth. The net was fished so that depth according to the monitor was within 100m of the bottom sounding at the position derived from triangulating back along the ship's track. All subsequent hauls up to 1000m off the bottom were fished using the monitor in this way. Table 1 gives the sounding ranges and mean soundings for these hauls. The depths of samples taken at up to 1000m off the bottom are expressed in terms of distance off the bottom. The depths of hauls shallower than 1000m off the bottom were taken directly from the monitor, i.e. measured from the surface.

The absolute depths fished using the techniques described are probably inaccurate, as both PES and monitor depths are subject to error due to the changes in water density and temperature, but they are accurate relative to both the bottom and each other. Any effect which the bottom may have on the bathypelagic animal populations is presumably proportional to their distance away from it, and these relative distances are consequently much more important ecologically than a possible error of a few metres in absolute depth. The changeover depth to conventional surface measurements was arbitrary. It may be shown subsequently that a distance of 1000m off the bottom is not the optimum changeover point although Brewer, Spencer, Biscaye, Hanley, Sachs, Smith, Radar & Fredericks (1976) have found that this distance is approximately the top of the nepheloid layer, at least further north in the Atlantic.

Most of the samples used here (Table 1) were taken at Station 9541 in April 1977, within an area 20°0·6′N to 20°25·4′N and 21°9·6′W to 21°56·4′W. These are the hauls described above. Station 9131 was fished in the same area in November 1976 as a preliminary to the detailed programme of April 1977. The near-bottom samples from this station were taken in a similar way to that described above but only a single bottom indicator switch was used.

## Material

The samples were preserved on the ship in 5% formalin. Subsequently they were transferred to a preserving fluid based on that of Steedman (1974) and the *Benthomisophria* spp. were picked out of the total RMT 1 and RMT 8 samples. A small triangular net (the DN) of mesh size 61µm was added to the RMT 1+8 combination net to sample small zooplankton. The DN catch was examined for one haul (9541 # 24) and contained 3 specimens of *B. palliata* and a single *B. cornuta.* All the material came from the hauls shown in Table 1 except for a single adult female *B. palliata* which was found in a RMT 8 sample fished between 3000 and 3500m in a position 44°27′N 12°44′W. The numbers of *B. palliata* and *B. cornuta* caught are given in Tables 2 and 3. No specimens of either species were found in hauls shallower than 2000m.

Undamaged specimens were measured from the tip of the cephalothorax to the end of the caudal rami. The numbers measured are also given in Tables 2 and 3. There was no difference in the size distribution of either species between stations 9131 and 9541 and data from both stations have been combined in the frequency distributions of body length (Figs 14 & 15).

**Table 2** The numbers of each stage of *Benthomisophria palliata* found and measured.

| Net | RMT 1 | | | | | | | RMT 8 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Stage<br>Station | I | II | III | IV | V | ♀ | ♂ | IV | V | ♀ | ♂ |
| 9541#18 | | 38 | 13 | 41 | 14 | 16 | 11 | | 1 | 5 | 4 |
| 19 | | 7 | 10 | 63 | 17 | 39 | 38 | | 1 | 25 | 17 |
| 22 | | 5 | 9 | 12 | 13 | 22 | 4 | 2 | 5 | 7 | 1 |
| 24 | 7 | 44 | 17 | 15 | 15 | 13 | 17 | | 5 | 4 | 2 |
| 25 | | | 3 | 8 | 26 | 3 | 6 | | 1 | | 1 |
| 26 | 1 | 5 | 6 | 11 | 6 | 5 | 2 | | | 4 | |
| 27 | | | | | | 1 | | | | | |
| 9131#18 | | 8 | 16 | 26 | 10 | 8 | 4 | | 2 | 13 | 2 |
| 19 | 5 | 37 | 33 | 22 | 12 | 17 | 4 | 1 | 4 | 9 | 1 |
| 23 | not examined | | | | | | | | | 9 | 3 |
| 8509#20 | | | | | | | | | | 1 | |
| Total of RMT1, RMT8 + DN | 14 | 144 | 107 | 201 | 132 | 203 | 117 | | | | |
| No. measured | 14 | 133 | 98 | 151 | 103 | 186 | 93 | | | | |

**Table 3** The numbers of each stage of *Benthomisophria cornuta* found and measured.

| Net | RMT 1 | | | | |
|---|---|---|---|---|---|
| Stage | III | IV | V | ♀ | ♂ |
| Station | | | | | |
| 9541#18 | 1 | | 2 | 2 | 2 |
| 19 | | | | 1 | 1 |
| 22 | 1 | | 1 | 1 | |
| 24 | | 2 | | 1 | 1 |
| 25 | | | 1 | 1 | |
| 26 | | | 3 | 3 | |
| 9131#18 | | 4 | 4 | 1 | |
| 19 | 1 | 3 | | | 2 |
| Total inc. DN | 4 | 9 | 11 | 10 | 6 |
| No. measured | 4 | 9 | 11 | 10 | 6 |

The copepods were stained in chlorazol black in lactophenol, dissected and examined in lactophenol and mounted as permanent preparations in polyvinyl lactophenol. They were examined by phase contrast microscopy and drawings were made with the aid of a camera lucida.

## Descriptions

### Family **MISOPHRIIDAE**

### Genus ***BENTHOMISOPHRIA***

### ***Benthomisophria palliata*** SARS, 1909

*Benthomisophria palliata* G. O. Sars, 1909: 1–4, Fig. 1.
*Misophria japonica* O. Tanaka, 1966: 51–55, Figs 1–2.
The descriptions of the adults of both sexes and of the copepodid stages of *B. palliata* are based on the examination of a total of 918 specimens. The specimens were sorted, on morphological criteria, into copepodid stages I to V, adult male and adult female.

COPEPODID I

Prosome (Fig. 1A) large, 5-segmented and comprising 86% of total body length; rounded anteriorly, with greatest width at posterior border of cephalosome. Last prosome somite with parallel sides and small postero-lateral projections. Urosome 1-segmented, sub-rectangular. Caudal rami apparently bearing only 1 dorsal and 2 distal armature elements.

First antenna (Fig. 1B) 6-segmented; with incomplete armature, elements present as follows: I – 2+1 spine, II – 1 aesthete, III – 0, IV – 0, V – 1, VI – 6. Second antenna (Fig. 1C) biramous with 5-segmented exopod and 3-segmented endopod, first segment of which is partially fused to basis. Labrum large, fused to rostrum. Mandible (Fig. 1D) blade with 4 large teeth and several other elements; mandibular palp biramous, with 2-segmented endopod and 4-segmented exopod. First maxilla (Fig. 1E) gnathobase with 2 naked and 10 spinulate setae; rudimentary outer lobe on basal segment bearing at least 3 setae; inner lobes 1 and 2 about equal in size and armed with 4 and 3 setae respectively; distal endopod segment with at least 3 distal setae (some elements missing), proximal segment also with 3 distal setae; exopod 1-segmented, armature incomplete. Second maxilla (Fig. 1F) apparently 5-segmented: first segment with 2 inner lobes both armed with 3 setae; second segment with

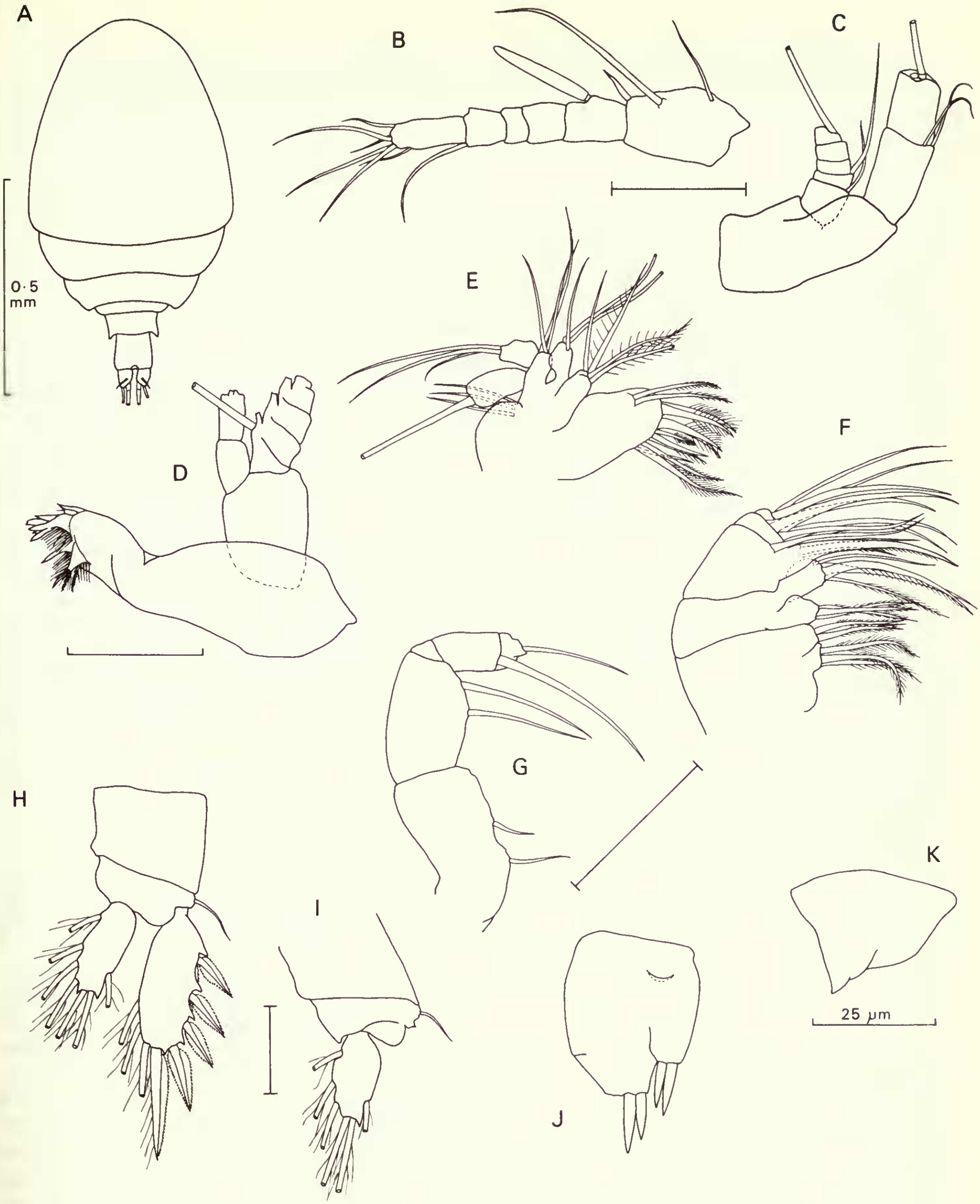


**Fig. 1** *B. palliata* Copepodid I. A, dorsal; B, first antenna; C, second antenna; D, mandible; E, first maxilla; F, second maxilla; G, maxilliped; H, Leg 1; I, leg 2; J, leg 3; K, leg 4. Scales 100µm unless otherwise indicated.

2 inner lobes bearing 3 and 4 setae; third segment extended medially into a large curved process carrying 2 setae basally; two distal segments bearing a total of 10 setae. Maxilliped (Fig. 1G) 5-segmented, armature incomplete in all available specimens.

Thoracic legs 1 to 4 present; legs 1 and 2 biramous, leg 3 bilobed and leg 4 rudimentary. Leg 1 (Fig. 1H) with 2-segmented sympod and 1-segmented rami; exopod bearing 4 outer margin spines, an apical spine and 3 inner margin setae; endopod with 1 outer, 2 distal and 4 inner margin setae. Leg 2 (Fig. 1I) segmentation as for leg 1; exopod missing in all specimens; endopod with 1 outer, 2 distal and 3 inner margin setae. Leg 3 (Fig. 1J) a broad flattened structure, bilobed distally with each lobe bearing 2 apical armature elements. Leg 4 (Fig. 1K) rudimentary, comprising a spinous process on a broad base.

Body length ranging from 0·69 to 0·95mm, with a mean of 0·79mm (based on 14 specimens).

COPEPODID II

Prosome (Fig. 2A) large, 4-segmented; first pedigerous somite incorporated into cephalosome, but with some indication of surture line marking the boundary. Urosome (Fig. 2B) 2-segmented; first segment with small processes at postero-lateral angles, second segment sub-rectangular. Caudal rami with 1 dorsal, 1 lateral and 2 distal elements.

First antenna (Fig. 2C) 9-segmented; armature incomplete, elements present as follows: I – 4, II – 0, III – 1 spine, IV – 1 aesthete, V – 1, VI – 1, VII – 0, VIII – 2, IX – 6 + 1 aesthete. Second antenna as in copepodid stage I but with exopod apparently comprising 5 distinct segments (Fig. 2D) and possibly a sixth segment fused to the basis; each of first 4 distinct segments bearing 1 seta, terminal segment with at least 1 element. Labrum, mandibles, maxillae and maxilliped as in adult.

Leg 1 (Fig. 2E) biramous, with 2-segmented rami; exopod segment 1 with 1 outer spine, inner seta missing; exopod segment 2 missing; endopod segment 1 with 1 inner seta, segment 2 with 1 outer, 2 distal and 4 inner margin setae. Leg 2 (Fig. 2F) as for leg 1 except endopod segment 2 with only 3 inner margin setae. Leg 3 (Fig. 2G) with 2-segmented sympod, biramous but with both rami missing in all specimens. Leg 4 (Fig. 2H) a flattened structure, bilobed distally with each lobe carrying 2 apical armature elements.

Body length ranging from 0·76 to 1·33mm, with a mean of 1·03mm (based on 133 specimens).

COPEPODID III

Prosome (Fig. 2I) large, 4-segmented, with first pedigerous somite fully incorporated into cephalosome. Urosome (Fig. 2J) 3-segmented; first segment with leg 5 present, second segment with rudiment of leg 6 present, third segment sub-rectangular. Caudal rami with 6 armature elements.

First antenna (Fig. 2K) 12-segmented; armature incomplete, elements present as follows: I – 1, II – 7, III – 2, IV – 0, V – 1, VI – 1 spine, VII – 1 + 1 aesthete, VIII – 1, IX – 1, X – 0, XI – 1, XII – 6 + 1 aesthete. Second antenna, labrum, mandible, maxillae and maxilliped as in adult.

Leg 1 (Fig. 3A) biramous, with 2-segmented rami; exopod segment 1 with 1 outer spine and 1 inner seta, segment 2 with 3 outer spines, 1 apical spine and 4 inner margin setae; endopod segment 1 with 1 inner seta, segment 2 with 1 outer, 2 distal and 5 inner margin setae. Leg 2 (Fig. 3B) as for leg 1 except exopod segment 2 missing in all specimens, and endopod segment 2 with only 4 inner margin setae. Leg 3 (Fig. 3C) with both rami 2-segmented but incomplete in material available. Leg 4 (Fig. 3D) with 2-segmented sympod, biramous but with both rami missing in all specimens.

Leg 5 (Fig. 2L) 1-segmented, with 1 inner proximal and 3 distal setae. Leg 6 (Fig. 2M) represented by an unarmed spinous process.

Body length ranging from 0·99 to 1·71mm, with a mean of 1·29mm (based on 98 specimens).

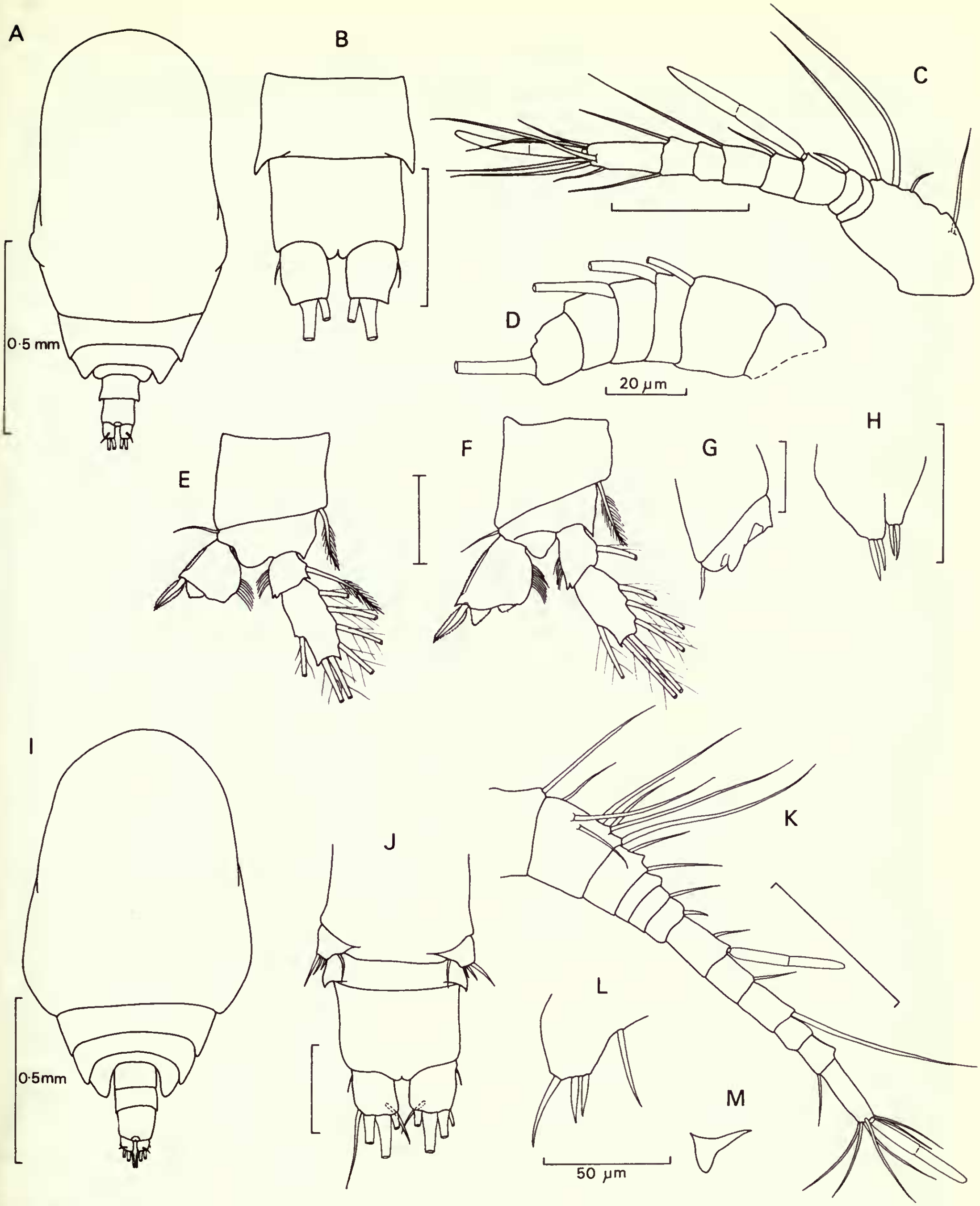


**Fig. 2** *B. palliata* Copepodid II & III. A, Copepodid II, dorsal; B, urosome, ventral; C, first antenna; D, exopod of second antenna; E, leg 1; F, leg 2; G, leg 3; H, leg 4; I, Copepodid III, dorsal; J, urosome, ventral; K, first antenna; L, leg 5; M, leg 6. Scales 100µm unless otherwise indicated.

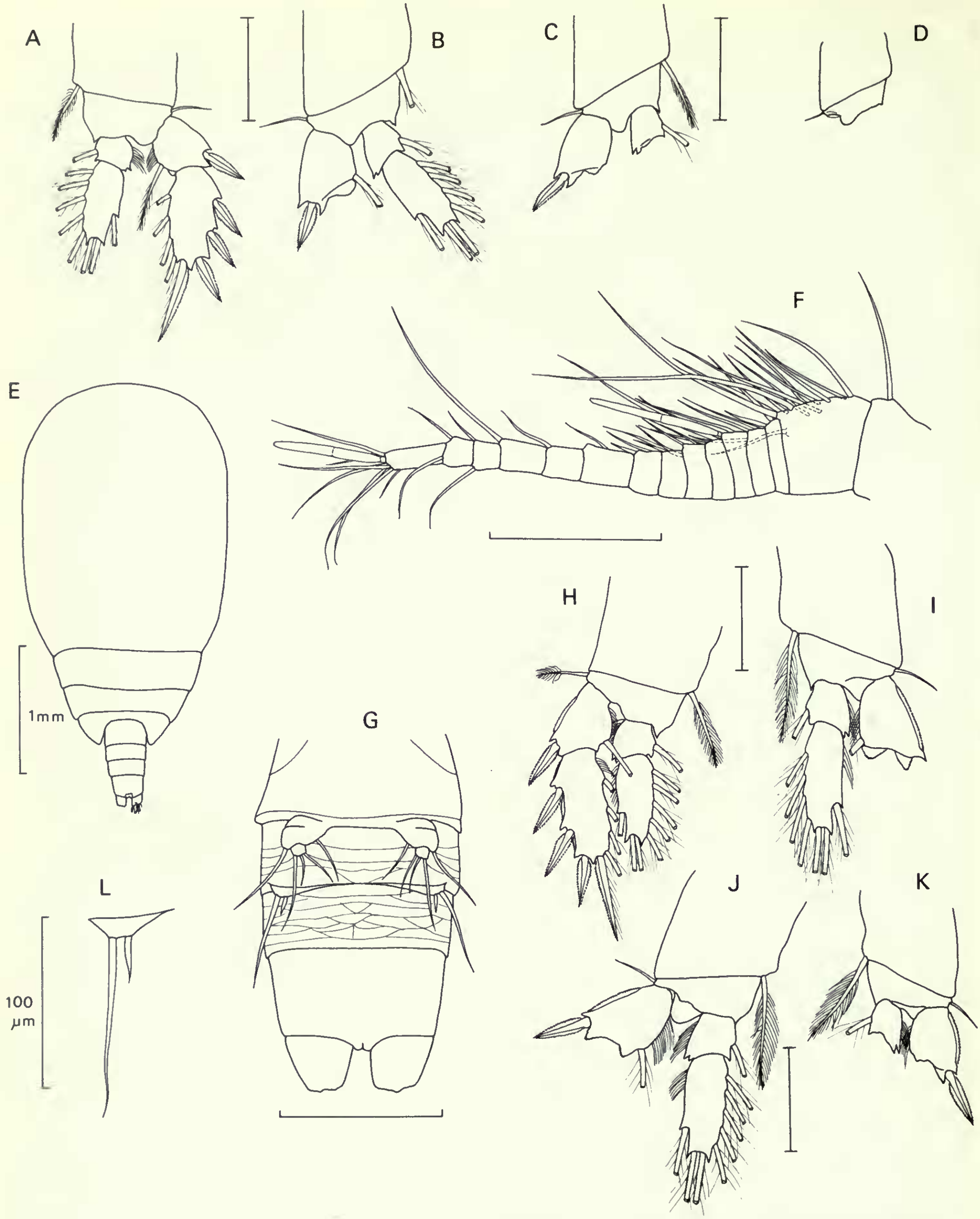


**Fig. 3** *B. palliata* Copepodid III & IV. A, Copepodid III leg 1; B, leg 2; C, leg 3; D, leg 4; E, Copepodid IV, dorsal; F, first antenna; G, urosome, ventral; H, leg 1; I, leg 3; J, leg 2; K, leg 4; L, leg 6. Scales 200µm unless otherwise indicated.

### Copepodid IV

Prosome (Fig. 3E) large, 4-segmented. Urosome (Fig. 3G) 4-segmented; first and second segments bearing legs 5 and 6 respectively; segments 1 to 3 all with conspicuous reticulate surface markings; urosome segment 4 without surface markings.

First antenna (Fig. 3F) 15-segmented; armature elements present as follows; I – 1, II – 12, III – 2, IV – 3, V – 2 + 1 aesthete, VI – 2, VII – 3 + 1 aesthete (missing from figured specimen), VIII – 2, IX – 1 + 1 spine, X – 1, XI – 1, XII – 1, XIII – 2, XIV – 2, XV – 7 + 1 aesthete. Second antenna, labrum, mandible, maxillae and maxilliped as in adult.

Leg 1 (Fig. 3H) and leg 2 (Fig. 3J) as in Copepodid III stage, except endopod segment 2 of leg 2 now with 5 inner margin setae. Leg 3 (Fig. 3I) exopod segment 1 with 1 outer spine and 1 inner seta, segment 2 missing in all specimens; endopod segment 1 with 1 inner seta, segment 2 with 1 outer, 2 distal and 4 inner margin setae. Leg 4 (Fig. 3K) biramous, both rami 2-segmented, armature and rami incomplete in all available specimens.

Leg 5 (Fig. 3G) 2-segmented; basal segment with indication of subdivision laterally and armed with 1 inner and 1 outer seta; second segment with 3 apical setae. Leg 6 (Fig. 3L) a small process with 1 long and 1 short apical seta.

Body length ranging from 1·41 to 2·55mm, with a mean of 1·88mm (based on 151 specimens).

### Copepodid V

Prosome (Fig. 4A) large, 4-segmented, with epimeral plates of last free thoracic somite not acutely pointed. Urosome 5-segmented; segments 1 to 4 with reticulate surface markings, segment 5 without surface markings. Caudal rami (Fig. 4B) with 6 armature elements.

First antenna (Fig. 4C) 17-segmented, armature elements present as follows: I – 1, II – 10, III – 2, IV – 8, V – 1 + 1 aesthete, VI – 2, VII – 1 + 1 aesthete, VIII – 2, IX – 2, X – 2, XI – 2, XII – 2, XIII – 1, XIV – 0, XV – 2, XVI – 2 + 1 aesthete, XVII – 7 + 1 aesthete. Second antenna, labrum, mandible, maxillae and maxilliped as in adult.

Legs 1 to 4 (Figs 4D–G) biramous, with 3-segmented rami; armature formula as follows:

| | coxa | basis | endopod | exopod |
|---|---|---|---|---|
| leg 1 | 0 – 1 | 1 – 0 | 0 – 1 ; 0 – 2 ; 1,2,3 | I – 1 ; I – 1 ; missing |
| leg 2 | 0 – 1 | 1 – 0 | 0 – 1 ; 0 – 2 ; 1,2,3 | I – 1 ; I – 1 ; III,I,5 |
| leg 3 | 0 – 1 | 1 – 0 | 0 – 1 ; 0 – 2 ; missing | I – 1*; I – 1; missing |
| leg 4 | 0 – 1 | 1 – 0 | 0 – 1 ; 0 – 2* ; missing | I – 1 ; I – 1 ; missing |

*elements missing but presumed present.

Leg 5 (Fig. 4H) as in adult. Leg 6 (Fig. 4I) a process armed with an outer plumose seta and 2 unequal apical elements.

Body length ranging from 2·01 to 3·75mm, with a mean of 2·71mm (based on 103 specimens).

### Adult male

Prosome (Fig. 5A) comprising 70 to 75% of total body length; epimeral plates of last free thoracic somite produced posteriorly and provided with expanded hyaline areas laterally. Urosome 6-segmented; segments 1 to 5 with reticulate surface markings (not figured), segment 6 with surface denticulations.

First antenna (Fig. 4J) apparently 16-segmented and geniculate, with the articulation between segments XIV and XV; aesthetes present on segments I, II (2), III, V, VII, X, XI, XIII, XV and XVI (2); segment XV also with a long spiniform process originating near base of aesthete; other armature elements present but omitted from figure.

All other appendages as for adult female except leg 6. Leg 6 (Fig. 5E) a process with a plumose outer seta, a long plumose apical seta and a short inner spiniform element.

Body length of males ranging from 2·70 to 4·72mm, with a mean of 3·75mm (based on 93 specimens).

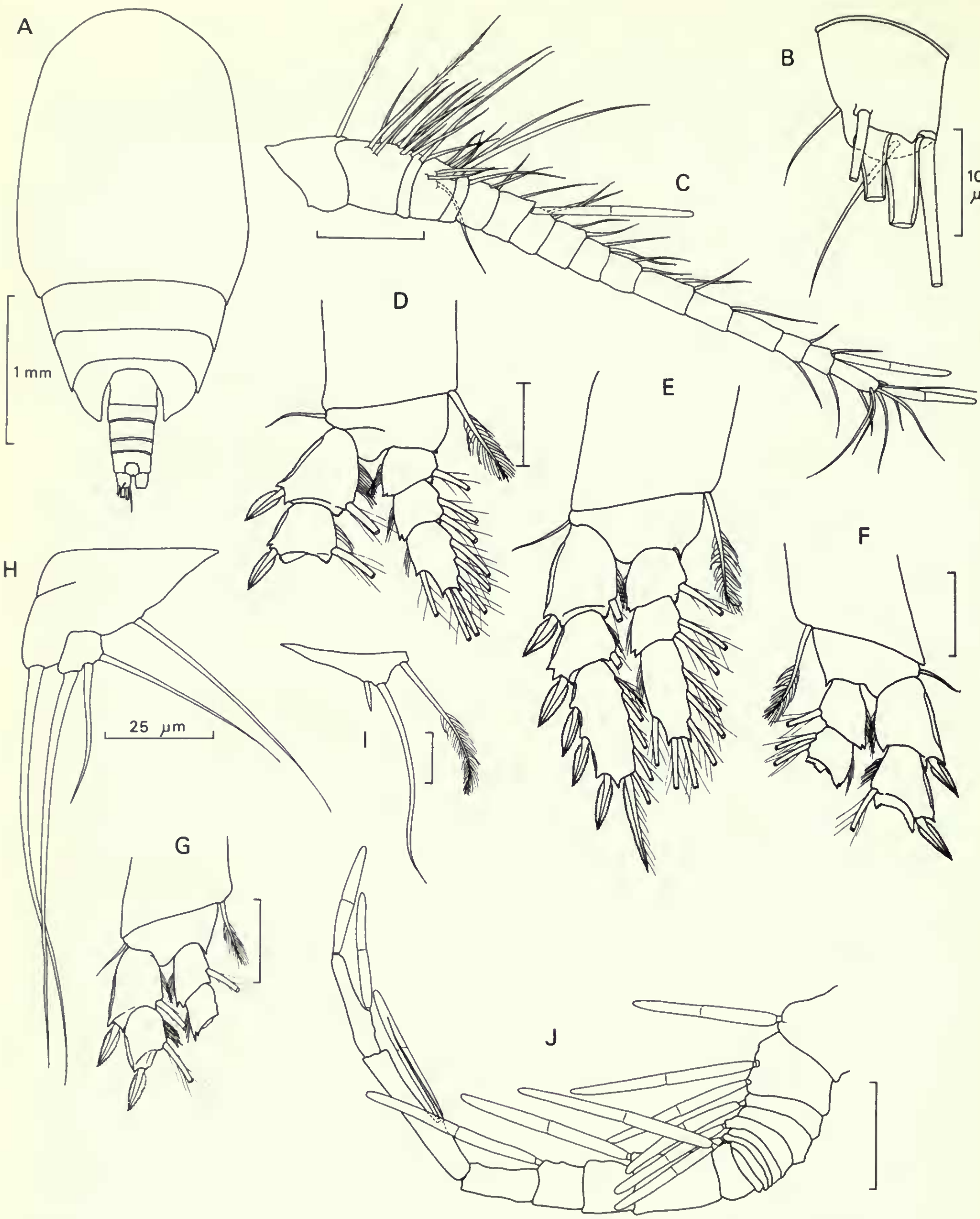


**Fig. 4** *B. palliata* Copepodid V & adult male. A, Copepodid V, dorsal; B, caudal ramus, ventral; C, first antenna; D, leg 1; E, leg 2; F, leg 3; G, leg 4; H, leg 5; I, leg 6; J, Adult male first antenna (with setae omitted). Scales 200µm unless otherwise indicated.

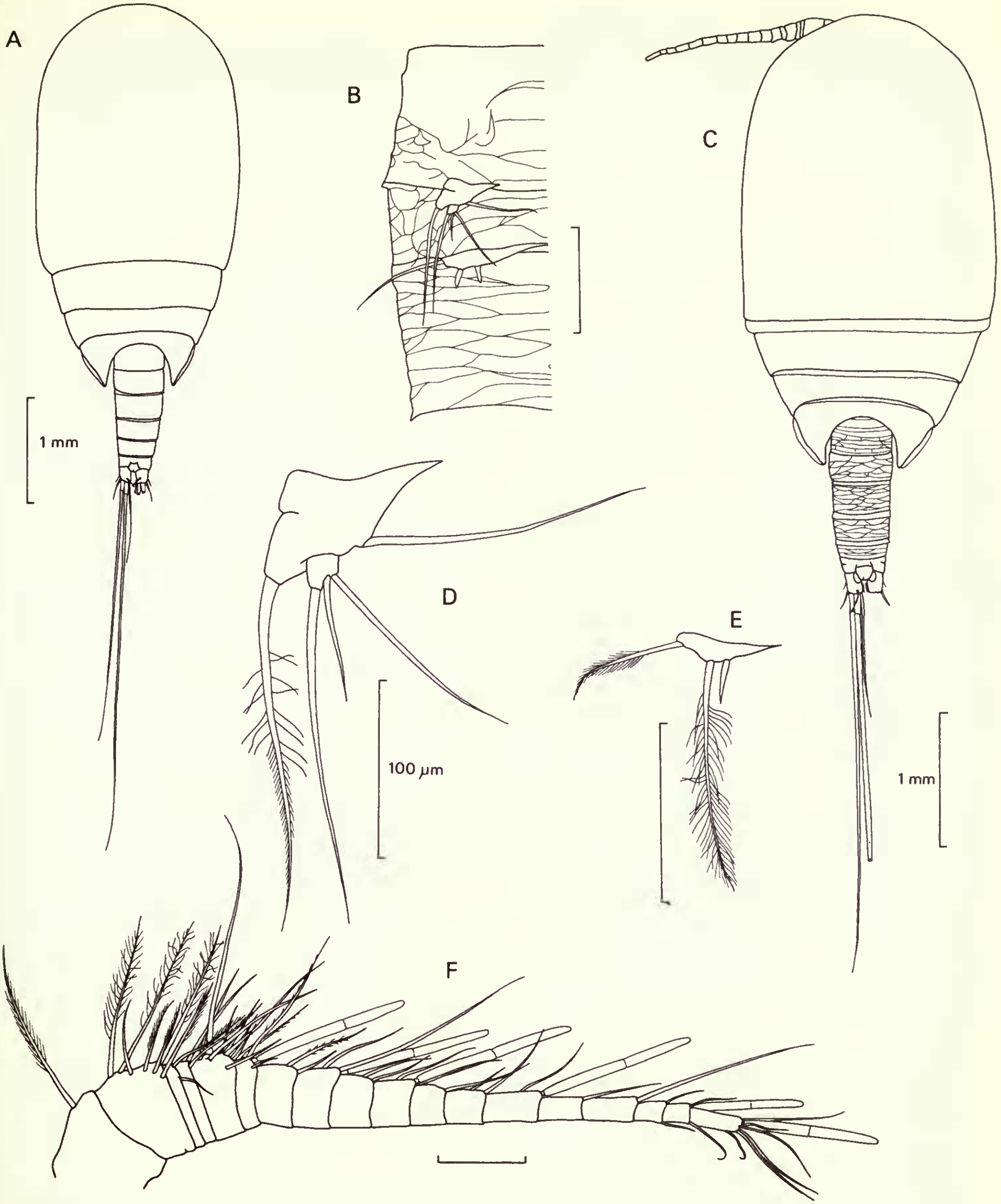


**Fig. 5** *B. palliata* Adult male & female. A, Male, dorsal; B, Female urosome, ventral; C, Female, dorsal; D, leg 5; E, Male leg 6; F, Female first antenna. Scales 200µm unless otherwise indicated.

ADULT FEMALE

Prosome (Fig. 5C) large, 4-segmented with reticulate surface markings (not shown in Fig. 5C); segments 1 to 3 with strips of hyaline membrane dorsally along their posterior borders; segment 4 with posteriorly produced epimeral plates and with expanded hyaline areas laterally. Urosome (Fig. 5B) 6-segmented; segments 1 to 5 with reticulate surface markings, segment 6 with surface denticulations.

Labrum (Fig. 7B) strongly developed, fused to rostrum and projecting postero-ventrally from ventral body surface.

First antenna (Fig. 5F) 18-segmented; armature elements as follows: I – 1, II – 7, III – 2, IV – 2, V – 10, VI – 2 + 1 aesthete, VII – 2, VIII – 2 + 1 aesthete, IX – 2, X – 2 + 1 aesthete, XI – 1, XII – 2, XIII – 1 + 1 aesthete, XIV – 1, XV – 1, XVI – 2, XVII – 2 + 1 aesthete, XVIII – 6 + 1 aesthete.

Second antenna (Fig. 6A), basis with 1 outer distal seta; endopod 3-segmented, exopod with 5 distinct segments and possibly a sixth fused to basis. Endopod segment 1 with 1 outer margin seta, segment 2 with 3 outer margin setae and segment 3 with 6 long plumose apical setae. Exopod with 1 unilaterally pinnate seta on each of the first 4 distinct segments, and with 3 similar setae on terminal segment.

Mandible (Fig. 6B) blade with 8 main elements on distal margin (numbered 1–7 on Fig. 6B as element 8 is identical to element 7). Mandibular palp biramous, with 2-segmented endopod and 4-segmented exopod; endopod segments 1 and 2 bearing 1 and 2 setae respectively; exopod segments 1 to 4 bearing 1,1,1 and 3 long plumose setae respectively.

First maxilla (Fig. 6C) gnathobase with 15 elements; inner lobes 1 and 2 with 6 and 4 plumose setae respectively; outer lobe rudimentary, represented by 7 plumose setae on surface of segment; endopod apparently 2-segmented with distal segment positioned at an angle of 90° to proximal segment; proximal segment with 4 plumose setae apically, distal segment with 4 naked setae medially, 1 naked and 4 plumose setae apically; exopod 1-segmented, with 2 plumose setae medially and 5 long plumose setae distally.

Second maxilla (Fig. 6D–E) apparently 6-segmented; first segment with 5 plumose setae on proximal inner lobe and 3 on distal inner lobe; second segment with 2 inner lobes, each bearing 3 apical setae; third segment produced medially into a curved claw armed with 2 slender naked setae near its base; segments 4 to 6 bearing a total of 11 elements, 7 strong curved setae armed with 1 or 2 rows of pinnules and 4 slender naked setae.

Maxilliped (Fig. 6F) apparently 5-segmented; first segment with a single pinnate seta on a raised denticulated area situated proximally on the medial surface, a group of 1 small naked seta and 2 pinnate setae on another raised denticulated area in the middle, and 2 pinnate setae distally; second segment with a medial row of pinnules, 3 pinnate setae distally on medial margin and 3 areas of denticulations; third segment small and armed with a single pinnate seta; fourth segment partially subdivided into 3 portions each bearing 1 seta; fifth segment very small, bearing 4 slender setae.

Legs 1 to 4 (Figs 7C–F) biramous, with 3-segmented rami; armature formula as follows:

| | coxa | basis | endopod | exopod |
|---|---|---|---|---|
| leg 1 | 0 – 1 | 1 – 0 | 0 – 1 ; 0 – 2 ; 1,2,3 | I – 1 ; I – 1 ; III,I,4 |
| leg 2 | 0 – 1 | 1 – 0 | 0 – 1 ; 0 – 2 ; 1,2,3 | I – 1 ; I – 1 ; III,I,5 |
| leg 3 | 0 – 1 | 1 – 0 | 0 – 1 ; 0 – 2 ; 1,2,3 | I – 1 ; I – 1 ; III,I,5 |
| leg 4 | 0 – 1 | 1 – 0 | 0 – 1 ; 0 – 2 ; missing | I – 1 ; missing |

Pinnule rows present on lateral margins of all endopod segments and medial margins of all exopod segments. Lateral margins of all exopod segments armed with strips of serrated membrane. All outer margin spines bilaterally serrate, apical spines on exopods of legs 2 and 3 bilateraly serrate, that on leg 1 unilaterally serrate.

Leg 5 (Fig. 5D) 2-segmented; proximal segment with indication of suture line laterally, bearing a long outer seta apically and a medium length seta on inner margin; distal segment


**Fig. 6** *B. palliata* Adult female. A, second antenna; B, mandible – showing armature elements 1–7 enlarged; C, first maxilla – with rami separated from limb; D, second maxilla – showing segmentation; E, second maxilla with segments separated from each other; F, maxilliped. Scales 200μm unless otherwise indicated.

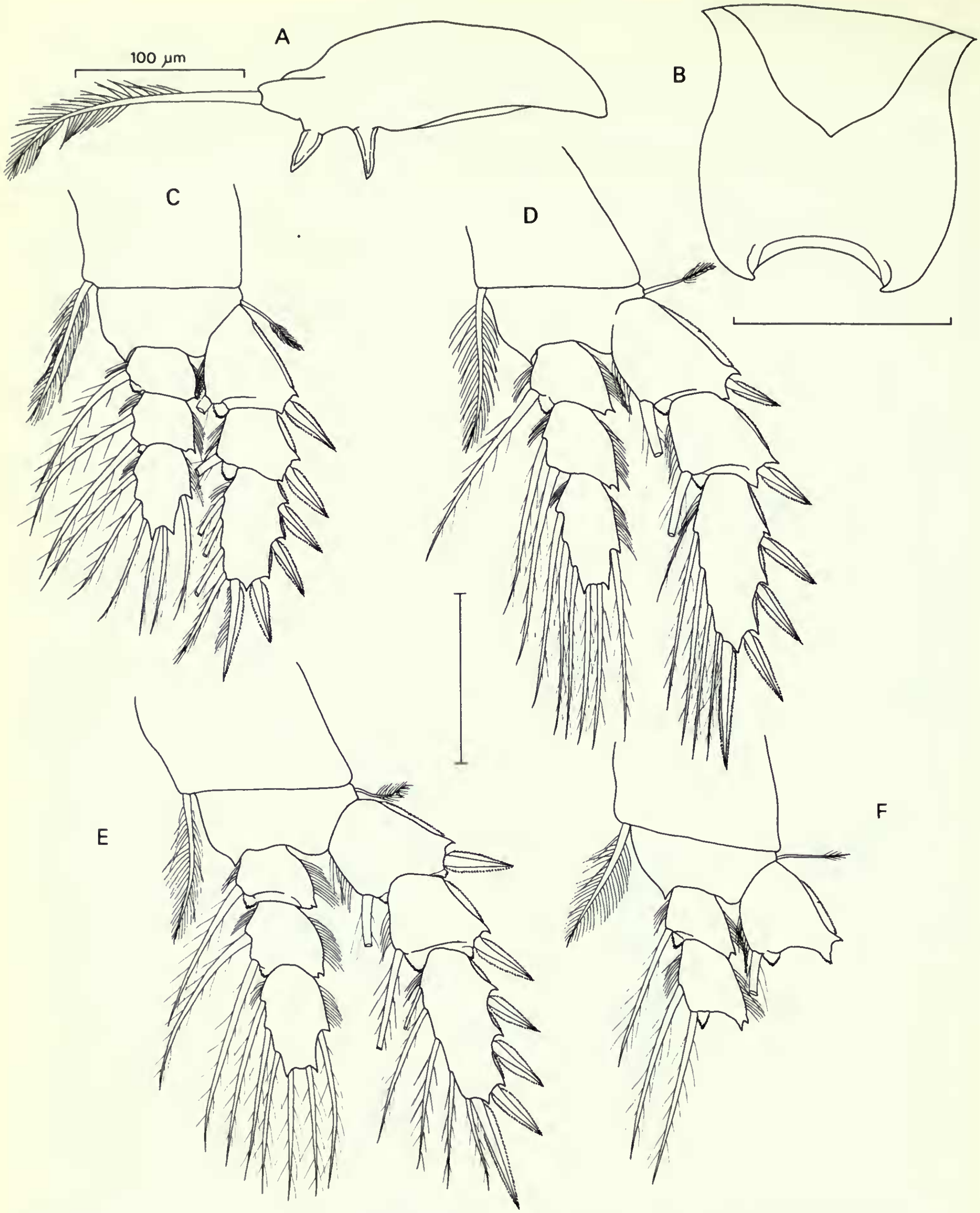


**Fig. 7** *B. palliata* Adult female. A, leg 6; B, labrum, ventral; C, leg 1; D, leg 2; E, leg 3; F, leg 4. Scales 0·5mm unless otherwise indicated.

bearing 3 unequal setae along oblique distal margin. Leg 6 (Fig. 7A) a broad plate produced into a small process laterally, bearing a long plumose seta on its apex, and with 2 short spiniform elements on lateral portion of posterior margin.

Body length of females ranging from 2·88 to 5·70mm, with a mean of 4·0mm (based on 186 specimens).

### Material examined

1♀, 1♂ and 1Co.V; S.A.S. *Le Prince Albert de Monaco,* Stn 2738 Côte W. du Portugal, 1908; donated by G. O. Sars, stored in the Musée Océanographique de Monaco.

203♀♀, 117♂♂, 132 Co.V, 201 Co.IV, 107 Co.III, 144 Co.II, 14 Co.I; 'Discovery' Stns 9541, 9131 and 8509 (see Table 2); BM(NH) registration numbers 1979.1–10 (♀♀), 1979.11–20 (♂♂), 1979.21–30 (Co.V), 1979.31–40 (Co.IV), 1979.41–50 (Co.III), 1979.51–60 (Co.II) and 1979.61–70 (Co.I).

### Remarks

A certain amount of confusion has been caused by inconsistencies in the original description of *B. palliata* (Sars, 1909). The type 'specimen' figured by Sars exhibits features characteristic of two different life cycle stages, i.e. the 6-segmented urosome of an adult female and the 17-segmented first antenna of a Copepodid V stage. It is probable that Sars added the first antennae to his drawing of the body of an adult female. In an attempt to resolve this situation Sars' material of *B. palliata,* stored in the Musée Océanographique de Monaco, was examined. This material comprises an adult female (with a 6-segmented urosome and 18-segmented first antenna), an adult male and a Copepodid V stage (with a 5-segmented urosome and 17-segmented first antenna). If this is the type material it would provide confirmation that Sars' figured 'specimen' combines features of both adult female and Copepodid V. However, it is not certain that this is the type material because the label with the material gives only one station (No. 2738) whereas Sars (1909) states that his 3 type specimens were taken at 3 separate stations (Nos. 819, 1479 and 2108).

*Misophria japonica* Tanaka, 1966 was described from one specimen of each sex and does not differ significantly from *B. palliata.* It is therefore regarded as a junior synonym. Tanaka's specimens were taken in a haul made between 1000–0m depth in the Pacific Ocean adjacent to the Izu region of Japan. This is the shallowest record of *B. palliata.*

## ***Benthomisophria cornuta*** Hulsemann & Grice, 1964

*Benthomisophria cornuta* K. Hulsemann & G. D. Grice, 1964: 259–260, Figs 1–15.
*Misophria maculata.* O. Tanaka, 1966: 55–56, Fig. 3.

The descriptions of the adults of both sexes and of the later copepodid stages of *B. cornuta* are based on the examination of a total of 40 specimens. The specimens were sorted, on morphological criteria, into copepodid stages III to V, adult male and adult female.

### Copepodid III

Prosome (Fig. 8A) large, 4-segmented, with the epimeral plates of the last two free thoracic somites produced posteriorly into acute projections. Urosome (Fig. 8B) 3-segmented; segments 1 and 2 bearing rudiments of legs 5 and 6 respectively. Caudal rami with 6 armature elements as in adult.

First antenna (Fig. 8C) 12-segmented; armature incomplete, elements present as follows: I – 1, II – 6, III – 2 + 1 aesthete, IV – 1, V – 1 + 1 aesthete, VI – 1 spine, VII – 0, VIII – 1, IX – 1, X – 1, XI – 1 + 1 aesthete, XII – 6 + 1 aesthete. Second antenna, labrum, mandible, maxillae and maxilliped as in adult.

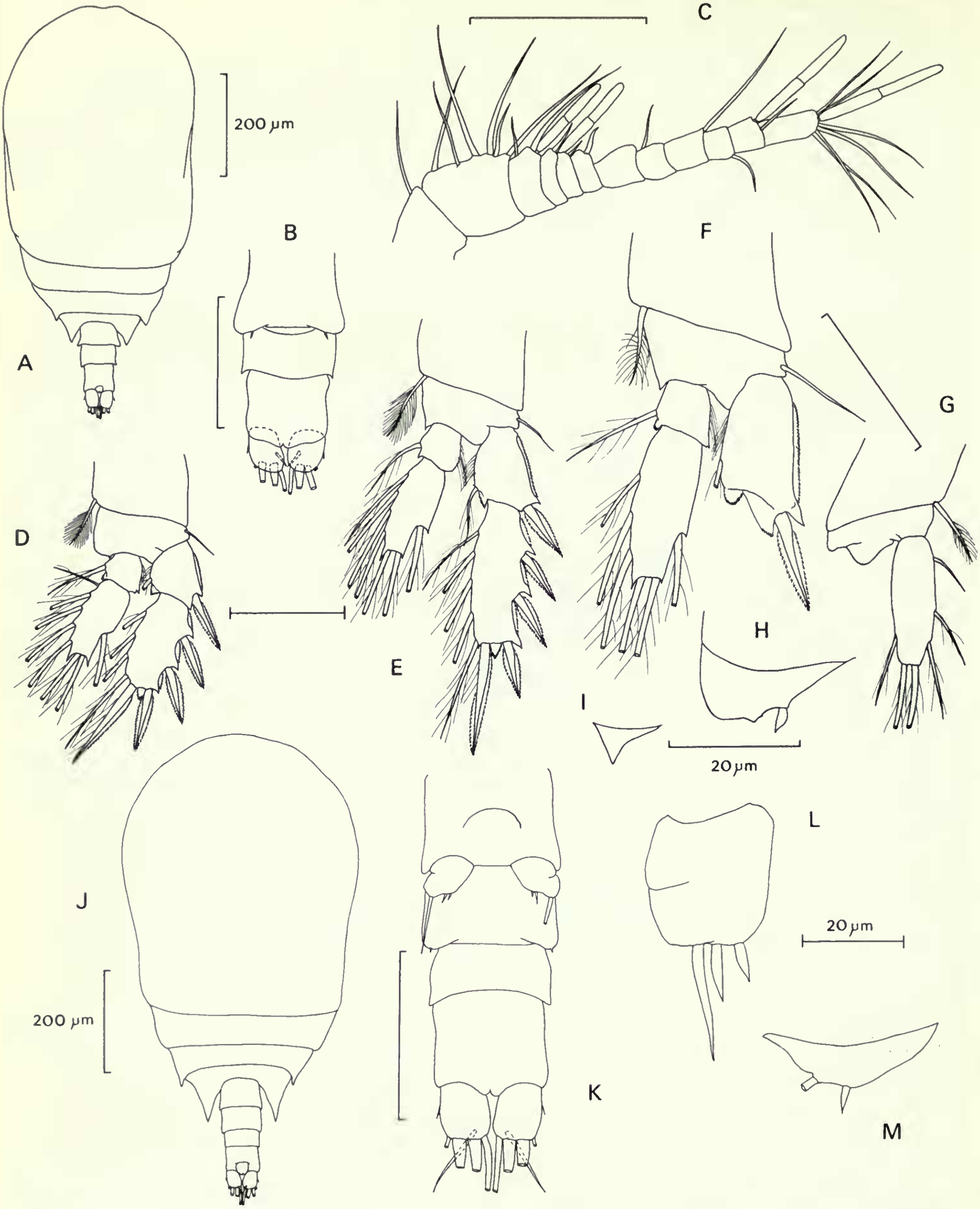


**Fig. 8** *B. cornuta* Copepodid III & IV. A, Copepodid III, dorsal; B, urosome, ventral; C, first antenna; D, leg 1; E, leg 2; F, leg 3; G, leg 4; H, leg 5; I, leg 6; J, Copepodid IV, dorsal; K, urosome, ventral; L, leg 5; M, leg 6. Scales 100μm unless otherwise indicated.

Legs 1 to 3 (Figs 8D–F) biramous, with 2-segmented rami; leg 4 (Fig. 8G) biramous with 1-segmented rami. Armature formula as follows:

| | coxa | basis | endopod | exopod |
|---|---|---|---|---|
| leg 1 | 0 – 1 | 1 – 0 | 0 – 1 ; 1,2,5 | I – 1 ; III,I,4 |
| leg 2 | 0 – 1 | 1 – 0 | 0 – 1 ; 1,2,4 | I – 1 ; III,I,5 |
| leg 3 | 0 – 1 | 1 – 0 | 0 – 1 ; 1,2,3 | I – 1 ; missing |
| leg 4 | 0 – 1 | 1 – 0 | 1,2,3 | missing |

All exopod segments bearing strips of serrated membrane laterally and all outer margin spines bilaterally serrate.

Leg 5 (Fig. 8H) a rounded process situated postero-laterally on first urosome somite, armed with a single rudimentary element subapically, another element may have been present but was missing from all specimens available for examination. Leg 6 (Fig. 8I) a small spinous process.

Body length ranging from 0·72 to 0·73mm, with a mean of 0·72mm (based on 3 specimens).

### Copepodid IV

Prosome (Fig. 8J) large, comprising about 75% of total body length; epimeral plates of somites 3 and 4 strongly produced posteriorly. Urosome (Fig. 8K) 4-segmented.

First antenna (Fig. 9A) 15-segmented, with armature elements present as follows: I – 1, II – 11, III – 1 + 1 spine, IV – 2, V – 3 + 1 aesthete, VI – 1, VII – 1 + 1 aesthete, VIII – 2, IX – 1 + 1 spine, X – 1 (+ ?), XI – 1, XII – 1, XIII – 2, XIV – 1 + 1 aesthete, XV – 5 + 1 aesthete. Second antenna, labrum, mandible, maxillae and maxilliped as in adult.

Legs 1 to 4 (Figs 9B–E) biramous, with 2-segmented rami; armature formula as follows:

| | coxa | basis | endopod | exopod |
|---|---|---|---|---|
| leg 1 | 0 – 1 | 1 – 0 | 0 – 1 ; 1,2,5 | I – 1 ; III,I,4 |
| leg 2 | 0 – 1 | 1 – 0 | 0 – 1 ; 1,2,5 | I – 1 ; III,I,5 |
| leg 3 | 0 – 1 | 1 – 0 | 0 – 1 ; 1,2,4 | I – 1 ; missing |
| leg 4 | 0 – 1 | 1 – 0 | 0 – 1 ; 1,2,3 | I – 1 ; missing |

Leg 5 (Fig. 8L) a sub-rectangular plate, incompletely subdivided by a transverse suture line; distal margin with 3 armature elements. Leg 6 (Fig. 8M) a broad, flat process with 2 armature elements.

Body length ranging from 0·77 to 0·92mm, with a mean of 0·85mm (based on 7 specimens).

### Copepodid V

Prosome (Fig. 9F) with epimeral plates on last two free thoracic somites strongly produced posteriorly; dorsal and lateral surfaces of prosome with reticulate surface markings as shown in Fig. 9G on the right hand lateral portion of the cephalosome. Urosome (Fig. 10A) 5-segmented; segments 1 to 4 with reticulate surface markings, segment 5 without surface markings.

First antenna (Fig. 10B) 16-segmented, with armature elements as follows: I – 1, II – 10, III – 9, IV – 2 + 1 aesthete, V – 2, VI – 2 + 1 aesthete, VII – 2, VIII – 2 + 1 aesthete, IX – 2, X – 2, XI – 2 + 1 aesthete, XII – 1, XIII – 1, XIV – 2, XV – 2 + 1 aesthete, XVI – 6 + 1 aesthete. Second antenna, labrum, mandible, maxillae and maxilliped as in adult.

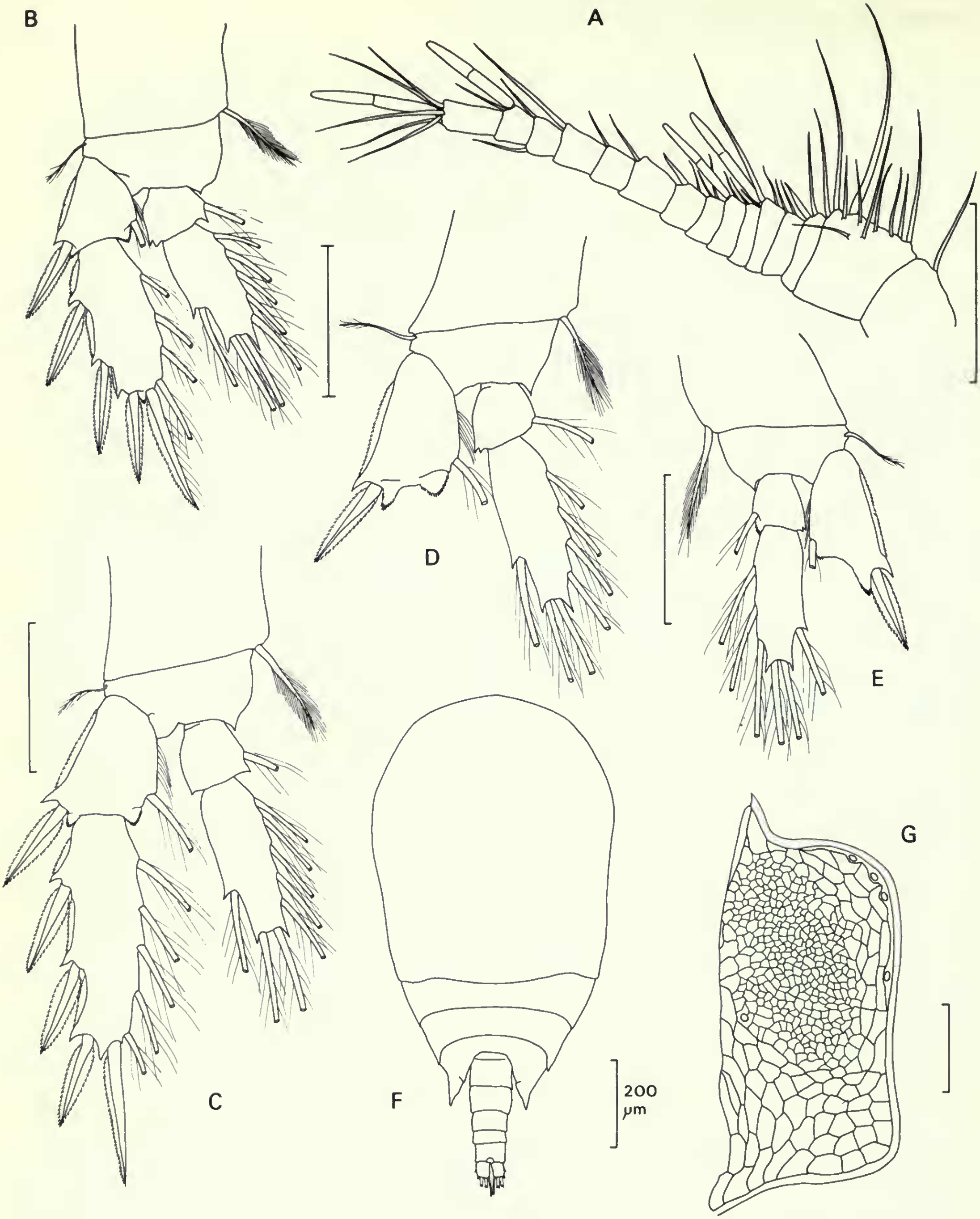


**Fig. 9** *B. cornuta* Copepodid IV & V. A, Copepodid IV first antenna; B, leg 1; C, leg 2; D, leg 3; E, leg 4; F, Copepodid V, dorsal; G, lateral portion of cephalosome – showing reticulate surface markings. Scales 100µm unless otherwise indicated.

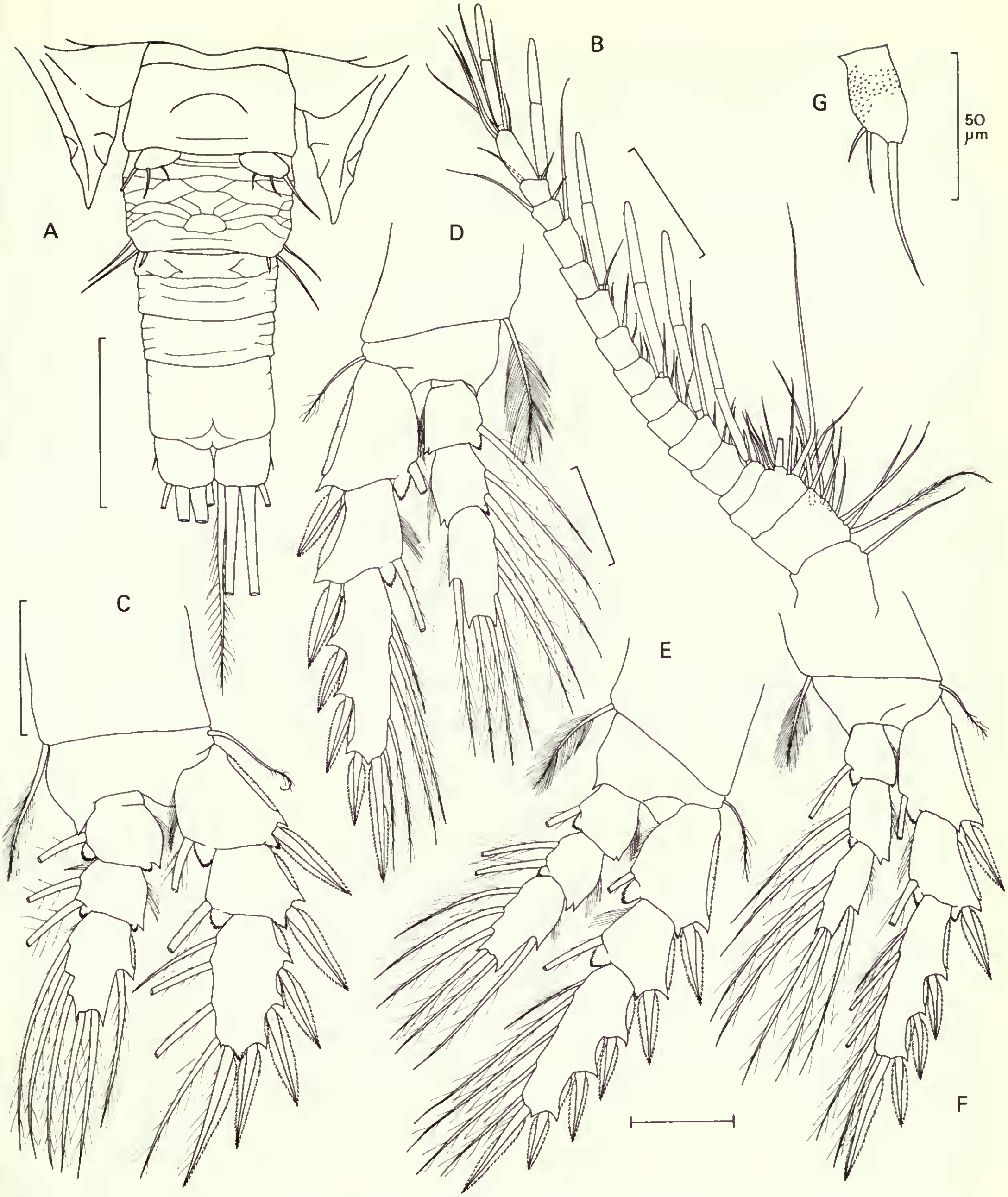


**Fig. 10** *B. cornuta* Copepodid V. A, urosome, ventral; B, first antenna; C, leg 1; D, leg 2; E, leg 3; F, leg 4; G, leg 5. Scales 100μm unless otherwise indicated.

Legs 1 to 4 (Figs 10C–F) biramous, with 3-segmented rami; armature formula as follows:

| | coxa | basis | endopod | exopod |
|---|---|---|---|---|
| leg 1 | 0 – 1 | 1 – 0 | 0 – 1 ; 0 –2 ; 1,2,3 | I – 1 ; I – 1 ; III,I,4 |
| leg 2 | 0 – 1 | 1 – 0 | 0 – 1 ; 0 –2 ; 1,2,3 | I – 1 ; I – 1 ; III,I,5 |
| leg 3 | 0 – 1 | 1 – 0 | 0 – 1 ; 0 –2 ; 1,2,3 | I – 1 ; I – 1 ; III,I,5 |
| leg 4 | 0 – 1 | 1 – 0 | 0 – 1 ; 0 –2 ; 1,2,2 | I – 1 ; I – 1 ; III,I,5 |

Lateral margins of all endopod segments except segment 3 of leg 1 with rows of pinnules; lateral margins of endopod segment 3 of leg 1 and all exopod segments armed with strips of serrated membrane.

Leg 5 (Fig. 10G) a single segment, with no indication of any subdivision, armed with a long naked apical seta and 2 short naked setae distally on the medial margin; some denticulations also scattered over surface. Leg 6 (Fig. 10A) represented by 1 short and 2 long setae.

Body length ranging from 0·85 to 1·10mm, with a mean of 1·0mm (based on 10 specimens).

### Adult male

Prosome (Fig. 11A) 4-segmented; epimeral plates of last two free thoracic somites strongly produced posteriorly; lateral indentations present on cephalosome (as in all other stages) allowing for movement of setae on mandibular palp and second antenna. Prosome with conspicuous reticulate surface markings both dorsally and laterally. Urosome (Fig. 11B) 6-segmented; segments 1 to 5 with reticulate surface markings, segment 6 without surface markings.

First antenna (Fig. 11D) apparently 16-segmented; geniculate,with articulation between segments XIV and XV; aesthetes present on segments I, II (2), III, V (2), VIII, IX, XI, XIII, XV and XVI (2); segment XV also with a long spiniform process originating near base of aesthete; other armature elements omitted from basal region in Fig. 11D for greater clarity. All other appendages as in adult female.

Body length of males ranging from 1·06 to 1·37mm, with a mean of 1·23mm (based on 6 specimens).

### Adult female

Prosome (Fig. 11G) 4-segmented, epimeral plates of last two free thoracic somites strongly produced posteriorly; surface of prosome with conspicuous reticulate surface markings (not figured) extending onto rostrum and labrum (Fig. 11C). Major reticulations on prosome divided into minute networks of fine markings, as shown on rostrum (Fig. 11C). Urosome 6-segmented, segments 1 to 5 with reticulate surface markings, segment 6 without markings.

Labrum (Fig. 11C) strongly developed, fused to rostrum; projecting postero-ventrally from ventral body surface, and with reticulate markings on ventral surface.

First antenna (Fig. 12A) 16-segmented; armature elements present as follows: I – 1, II – 9, III – 5, IV – 1 + 1 spine + 1 aesthete, V – 1, VI – 1 + 1 aesthete, VII – 0, VIII – 2 + 1 aesthete, IX – 1, X – 1, XI – 1 + 1 aesthete, XII – 1, XIII – 0, XIV – 2, XV – 2 + 1 aesthete, XVI – 7 + 1 aesthete.

Second antenna (Fig. 12B) basis with 1 outer distal seta; endopod 3-segmented and exopod with 5 distinct segments and possibly a sixth fused to basis. Endopod segment 1 unarmed, segment 2 with 4 outer margin setae, segment 3 with 1 outer margin seta and 6 long plumose apical setae. Exopod with 1 seta on each of first 4 distinct segments and with 3 setae on terminal segment.

Mandible (Fig. 12C) blade armed with 5 main teeth, 3 hirsute setae and a naked seta; mandibular palp biramous, with a 2-segmented endopod and 4-segmented exopod; endopod segments 1 and 2 bearing 2 and 6 setae respectively; exopod segments 1 to 4 bearing 2,1,1 and 2 long plumose setae respectively.

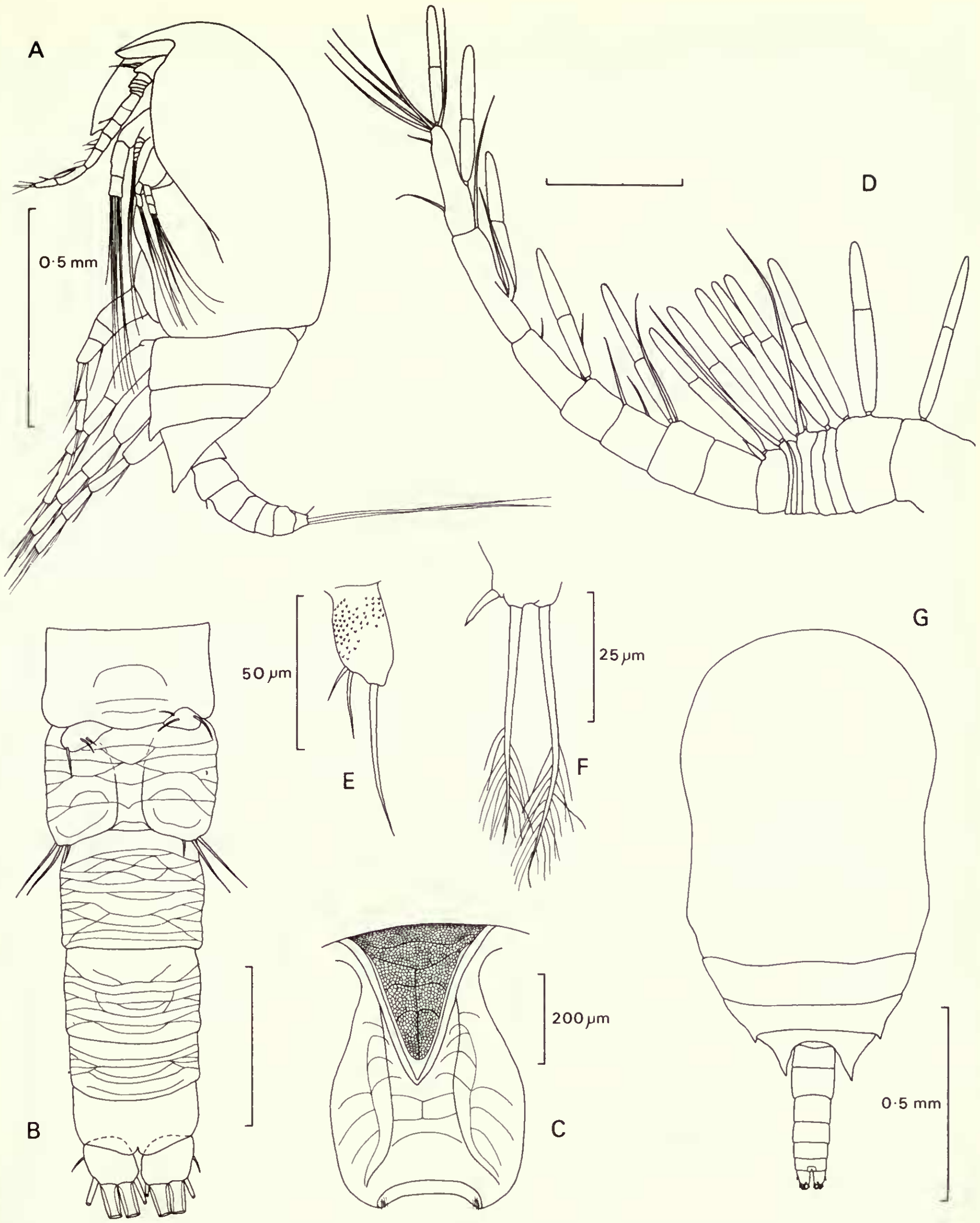


**Fig. 11** *B. cornuta* Adult male and female. A, Male, lateral; B, urosome, ventral; C, Female labrum, ventral; D, Male first antenna (with setae omitted from proximal portion); E, Female leg 5; F, leg 6; G, Female, dorsal. Scales 100μm unless otherwise indicated.

First maxilla (Fig. 12D) gnathobase with 15 armature elements; inner lobes 1 and 2 with 5 and 4 setae respectively; outer lobe rudimentary, represented by 6 plumose setae on surface of segment; endopod apparently 2-segmented with small distal segment positioned at an angle of 90° to proximal segment, proximal segment with 4 setae apically, distal segment with 2 naked setae medially and 1 naked and 2 plumose setae apically; exopod large, 1-segmented, with 6 plumose setae apically and 3 naked setae subapically on medial margin.

Second maxilla (Fig. 12E) apparently 6-segmented; first segment with proximal inner lobe bearing 4 plumose setae and distal inner lobe with 3 plumose setae; second segment with 2 inner lobes, each bearing 3 distal setae; third segment produced medially into a strong, slightly curved claw armed with 2 slender naked setae basally; distal 3 segments bearing a total of at least 8 elements.

Maxilliped (Fig. 12F) 5-segmented; first segment with 1 small naked seta and 2 plumose setae proximally and 2 plumose setae distally on medial margin; second segment with 3 plumose setae on medial margin; third segment small, bearing 1 seta; fourth segment with 4 setae; fifth segment reduced, armed with 5 setae.

Legs 1 to 4 (Figs 13A–D) biramous, with 3-segmented rami; armature formula as follows:

| | coxa | basis | endopod | exopod |
|---|---|---|---|---|
| leg 1 | 0 – 1 | 1 – 0 | 0 – 1;0 –2;1,2,3 | I – 1;I – 1;III,I,4 |
| leg 2 | 0 – 1 | 1 – 0 | 0 – 1;0 –2;1,2,3 | I – 1;I – 1;III,I,5 |
| leg 3 | 0 – 1 | 1 – 0 | 0 – 1;0 –2;1,2,3 | I – 1;I – 1;III,I,5 |
| leg 4 | 0 – 1 | 1 – 0 | 0 – 1;0 –2;missing | I – 1;I – 1;missing |

Pinnule rows present on lateral margins of all endopod segments and medial margins of exopod segments; lateral margins of all exopod segments and of endopod segment 3 of leg 3 armed with strips of serrated membrane; all outer margin spines bilaterally serrate, apical spine on exopods of legs 2 and 3 bilaterally serrate, that on leg 1 unilaterally serrate.

Leg 5 (Fig. 11E) 1-segmented, without trace of suture line; armed with 1 long naked apical seta and 2 short subapical setae on medial margin; denticulations scattered over surface of segment. Leg 6 (Fig. 11F) a simple process bearing 2 plumose setae on distal margin and a short spine at the disto-medial angle.

Body length of female ranging from 1·18 to 1·33mm, with a mean of 1·25mm (based on 9 specimens).

### Material examined

Holotype ♀; *Discovery* Stn 4768 (40°03′N 19°57′W), BM(NH) registration number 1964.7.10. Hulsemann and Grice, 1964.

10♀♀, 6♂♂, 11 Co.V, 9 Co.IV, 4 Co.III; *Discovery* Stns 9541 and 9131 (see Table 3); BM(NH) registration numbers 1979.71–80 (♀♀), 1979.81–86 (♂♂), 1979.87–97 (Co.V), 1979.98–106 (Co.IV) and 1979.107–110 (Co.III).

### Remarks

Hulsemann & Grice (1964) described the first antenna of this species as being 17-segmented, with the apical segment very small. The first antenna of the holotype on the prepared slide of the appendages (BM(NH) No. 1964.7.10) appears to have a seventeenth segment but examination of the other first antenna of the pair (figured in Fig. 12A) shows that the seventeenth segment of Hulsemann & Grice is actually the base of the apical aesthete and that this appendage is only 16-segmented.

This species is readily distinguishable from *B. palliata* on the basis of its small size, distinctive surface ornamentation, prolonged epimeral plates on the last 2 free thoracic somites, leg 5 and the segmentation of the first antenna.

There are no significant differences between *B. cornuta* and *Misophria maculata* Tanaka,

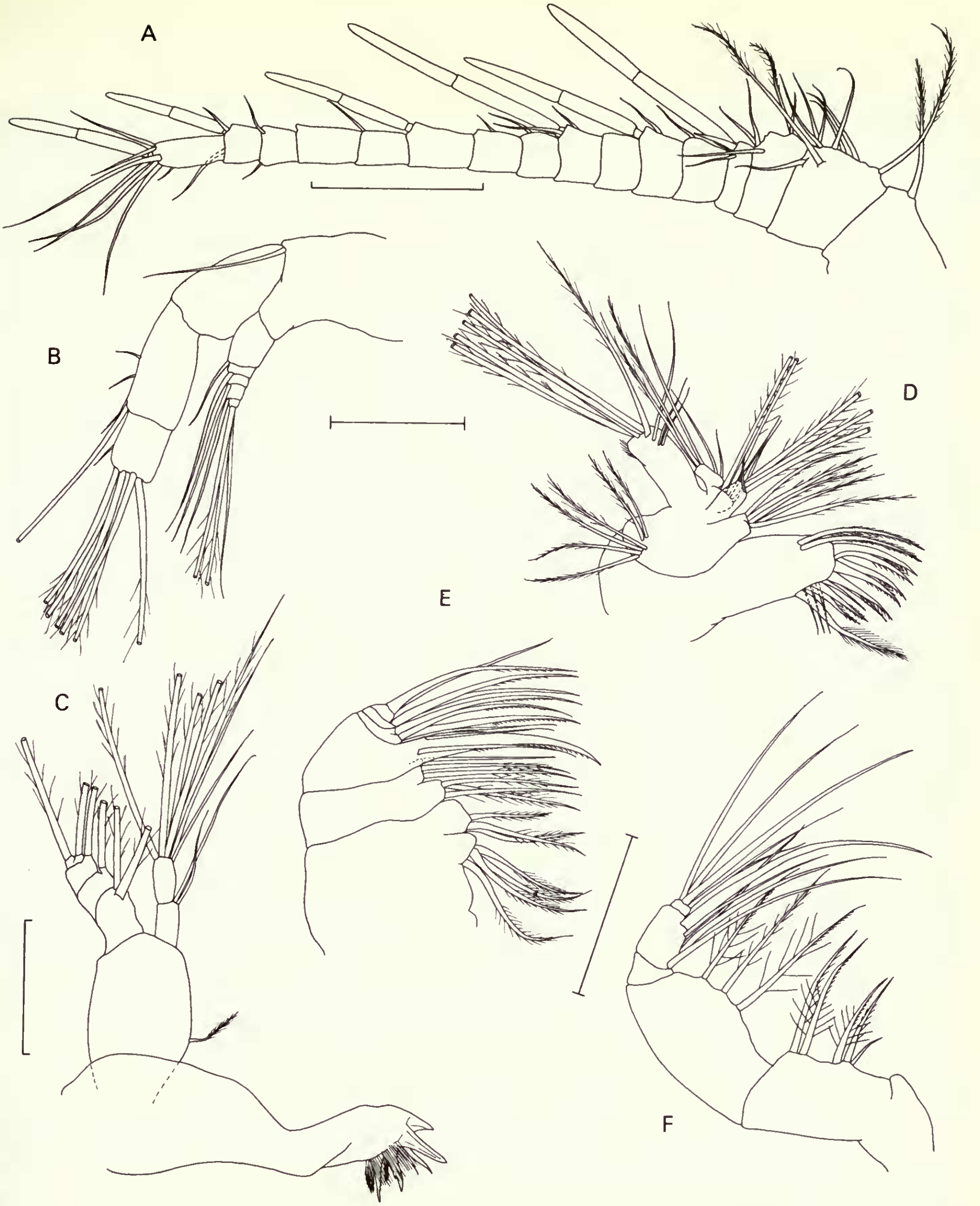


**Fig. 12** *B. cornuta* Adult female. A, Holotype ♀ (BM(NH) Reg. No. 1964.7.10), first antenna; B, Female second antenna; C, mandible; D, first maxilla; E, second maxilla; F, maxilliped. Scales 100μm.

1966. The slight differences between them can be accounted for largely by missing or damaged armature elements. *M. maculata* is therefore regarded as a junior synonym of *B. cornuta.* Tanaka's single female specimen was taken in a haul made between 1000–0m depth in the Pacific Ocean adjacent to the Izu region of Japan. This is the shallowest record of *B. cornuta.*

## Genus *MISOPHRIA*

### *Misophria pallida* Boeck, 1864

*Misophria pallida* A. Boeck, 1864: 248.

Gurney (1933) collected ovigerous female *M. pallida* and successfully hatched the eggs from them. He described the nauplius and copepodid I stages of this species. The descriptions given below are based on Gurney (1933).

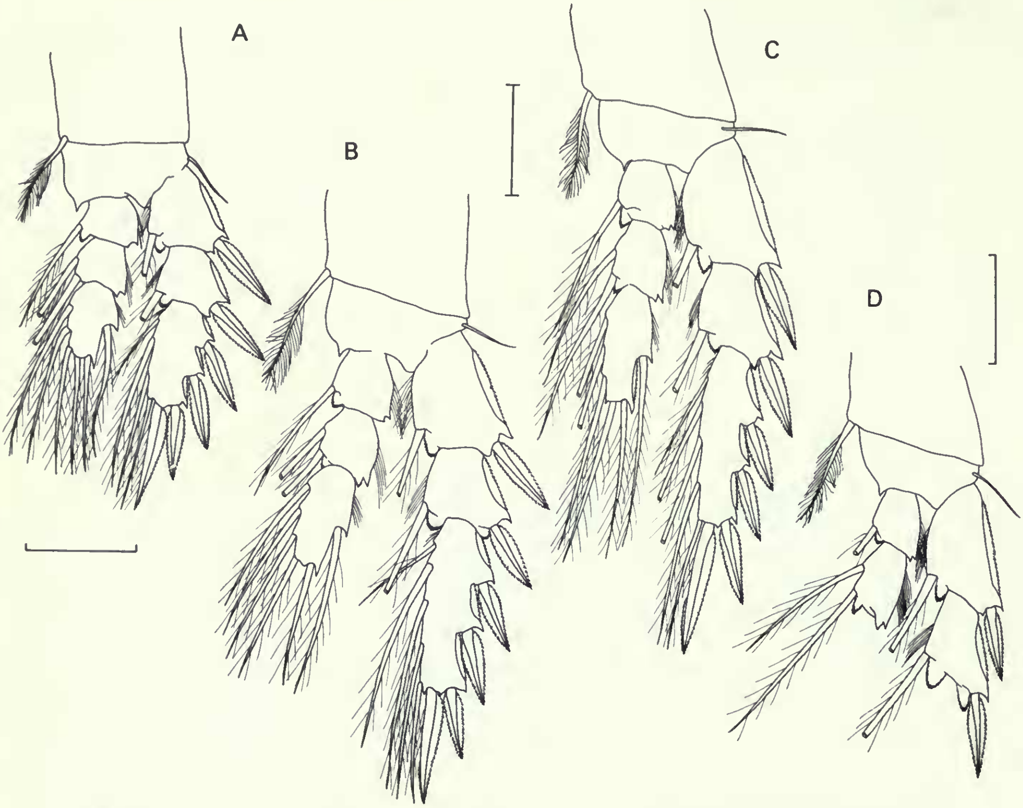


**Fig. 13** *B. cornuta* Adult female. A, leg 1; B, leg 2; C, leg 3; D, leg 4. Scales 100μm.

NAUPLIUS

Body rounded anteriorly, with maximum width at level of mandible. Eye absent. Mouth absent. Body filled with yolk. Appendages without gnathobases. First antenna uniramous and 2-segmented. Second antennae and mandibles biramous, with 4-segmented exopods. Rudiments of legs 1 and 2 visible through cuticle.

COPEPODID I

Body apparently as in *Benthomisophria palliata* copepodid I. Urosome 1-segmented. Caudal rami with 6 setae. First antenna 6-segmented. Labrum large. Second antenna, mandibles, first and second maxillae and maxillipeds present and similar in structure to those of the adult. Legs 1 and 2 biramous, with 2-segmented sympods and 1-segmented rami; armature formula for rami as follows:

| | endopod | exopod |
|---|---|---|
| leg 1 | 1, 2, 4 | IV, I, 3 |
| leg 2 | 1, 2, 2 (or 3?) | III, I, 2 |

Leg 3 a broad flattened structure, bilobed distally, bearing 2 small apical setae on outer lobe; inner lobe apparently unarmed. Leg 4 rudimentary, comprising a spinous process on a broad base.

REMARKS

The adult male and adult female are described in detail by Sars (1903). The similarities between the Copepodid I and the adult stages of *Misophria pallida* and *Benthomisophria palliata* suggest that development in these two genera follows a similar pattern through the copepodid stages. The nauplius of *Benthomisophria* is unknown but it may well resemble the yolky nauplius of *Misophria*.

Development in the Misophrioida appears to be characterized by only a single nauplius stage remaining in the life cycle. The yolk-filled non-feeding nauplius is short lived in *M. pallida,* moulting into the Copepodid I stage within about a day (Gurney, 1933). A similar type of lecithotrophic nauplius is found in many associated or parasitic copepods belonging to the orders Siphonostomatoida, Poecilostomatoida and Cyclopoida. The lecithotrophic nauplii possess more simply constructed appendages than those of the nauplii of free-living forms (Dudley, 1966). The lecithotrophic nauplius may represent an apomorphic character state, derived independently in several copepod orders as an adaption to an associated or parasitic mode of life. The adaptive significance of the presence of a single lecithotrophic nauplius in the life cycle of *M. pallida* (Misophrioida) will remain unknown until more data on the feeding biology and ecology become available for this species.

## Variation

### Body length

All the complete specimens of *B. palliata* were measured (Table 2) and the body length frequency distributions were calculated for all stages (Figs 14 & 15). The size range for each stage is extremely wide. In both adults and in the later copepodid stages the frequency distributions appear to be bimodal, indicating that two size groups are present within the population.

In the Copepodid V the modes are at 2·28 (2·24–2·32) and 2·96 (2·92–3·00)mm, in the adult male at 3·22 and 3·97mm and in the adult female at 3·30 and 4·35mm. There also appear to be traces of similar bimodality in the preceding copepodid IV and III stages, but more data are required to confirm this pattern. If the existence of a bimodal distribution at each stage from Copepodid III onwards is accepted, modes can be recognized at 1·22 and 1·52mm (Co.III), 1·75 and 2·05mm (Co.IV), 2·28 and 2·96mm (Co.V), 3·22 and 3·97mm (male) and 3·30 and 4·35mm (female). The proportional increase in body length from one stage to the next (for example, Co.III to Co.IV, or Co.V to female) of the small and/or the large form varies from 1·30 to 1·47 for each moult. These results indicate that the small and large size morphs persist from one moult to the next and, therefore, that a small Co.V would moult into a small adult male or adult female.

The small and large morphs differ only in size, no other morphological differences were observed between them. There is also a difference in the vertical distribution of the two morphs (page 37).

### Body shape

In addition to size dimorphism there is also considerable variation in the body shape of *B. palliata* individuals. Some specimens have a bloated, inflated appearance whereas others are much thinner. Swollen specimens are inflated both laterally and dorsally and have a distinct hump-backed appearance in lateral view (Figs 16D–E). Slim individuals have a much flatter dorsal profile (Figs 16B–C).

These changes in body proportions occur in both small and large individuals and do not correspond to changes in body length. In all other aspects of external morphology individuals of both types are identical. The gut, however, is very distended in swollen specimens

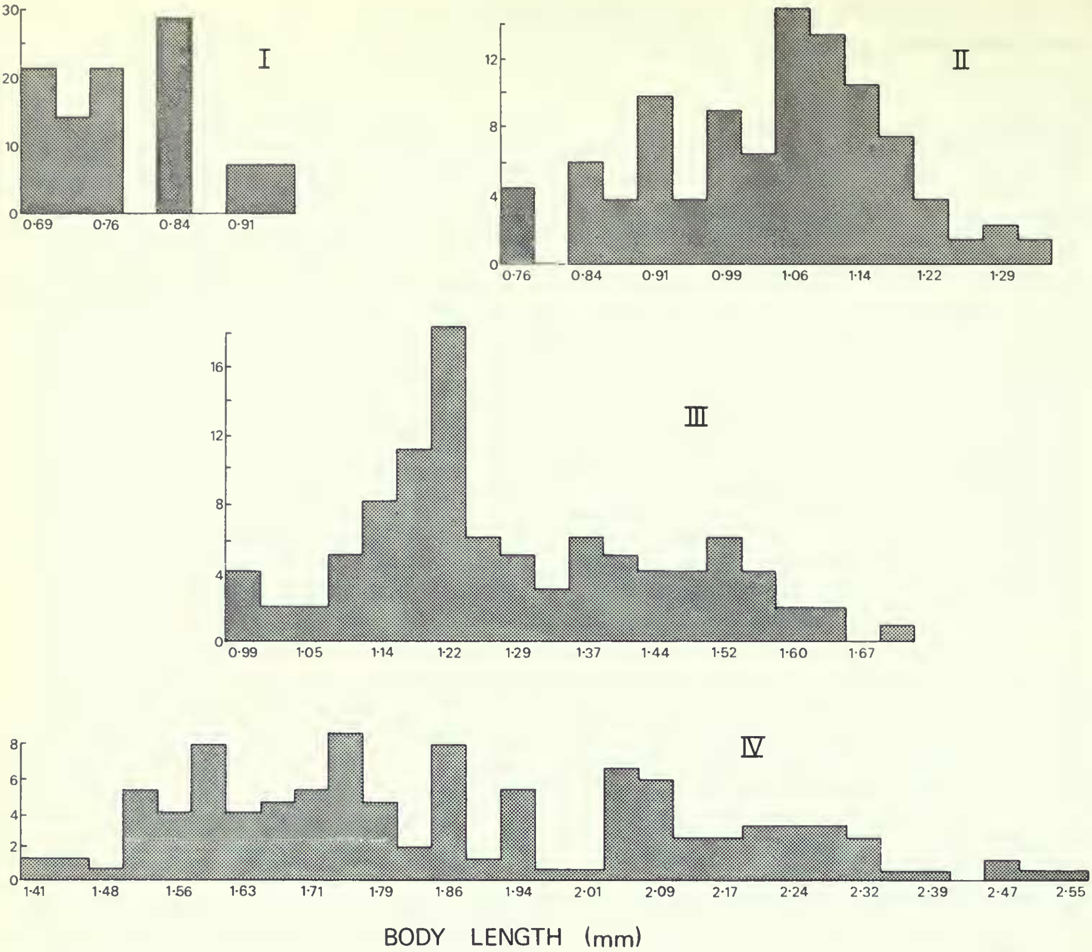


**Fig. 14** Size frequency distribution (in percent) of *B. palliata* Copepodid I – IV stages, using data from all measured specimens (see Table 2).

and is visible through the thin carapace virtually filling the entire prosome (Figs 16D–E). In slim individuals the gut is much smaller and cannot be seen through the carapace (Figs 16B–C).

The gut comprises a thin walled tube which is relatively wide in the prosome and is constricted just before entering the urosome. There is an anterior lobe extending into the head and two lateral lobes. In swollen individuals the gut is usually full (Figs 16F–G), in slim individuals it is empty (Fig. 16A). The gut contents are mainly small copepods, with a substantial amount of unidentifiable residue, mostly in the form of convoluted strings of tissue. The latter are possibly the remains of chaetognaths or coelenterates. A single radiolarian was also found.

The combination of a very elastic gut and a thin flexible integument enables *B. palliata* to gorge until its entire prosome is distended. The ornate pattern of surface markings on the exoskeleton of this species may facilitate this stretching. A similar gorging phenomenon has been observed in some species of abyssal amphipods (Shulenberger & Barnard, 1976, Thurston, 1979) and in the leptostracan *Nebaliopsis typica* (Rowett, 1943, Cannon, 1946). The ability to eat as much as possible when the opportunity arises is presumably a considerable advantage in areas, such as deep oceans, where food is scarce.

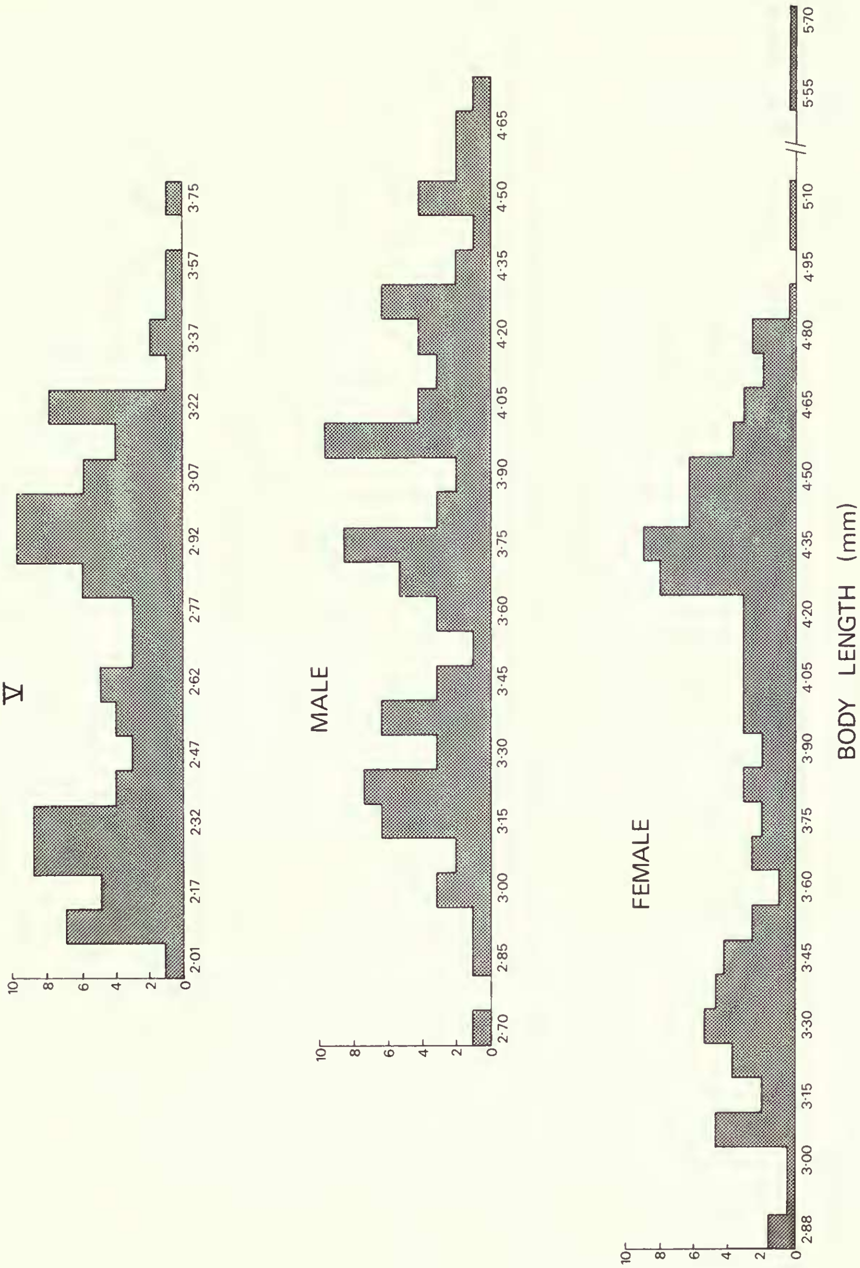


**Fig. 15** Size frequency distribution (in percent) of *B. palliata* Copepodid V and adults, using data from all measured specimens (see Table 2).

Similarly it is advantageous in such situations to be able to accurately locate a food supply. There is some evidence (Thurston, 1979) that copepods were attracted to a baited fish trap laid in a water depth of 4885m. The numerous large aesthetes on the first antennae of *B. palliata* probably have a chemosensory function. A chemosensory system will be necessary for the location of food in all post-naupliar stages. The large number of aesthetes on the first antennae of the adult male suggests that they also have a reproductive function, possibly enabling the male to locate a female. Other male copepods have been shown to respond to sex pheromones produced by the females, thereby demonstrating the existence of a chemosensory system (Katona, 1973).

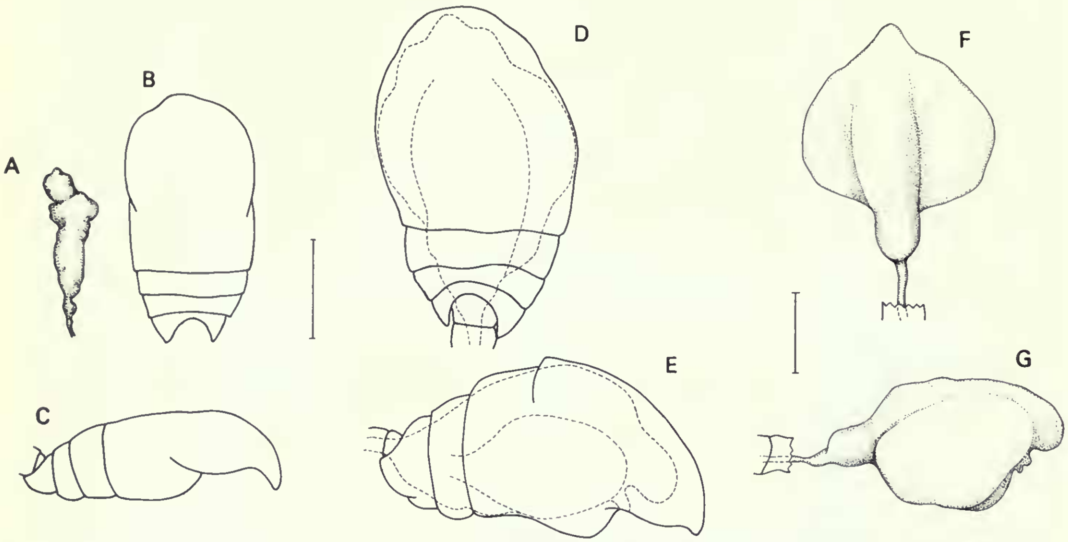


**Fig. 16** Variation in body shape in *B. palliata*. Slim specimen (♂ T.L. 3·22mm, Stn 9541 # 18) A, gut; B, prosome, dorsal; C, prosome, lateral. Swollen specimen (♀ T.L. 4·27mm, Stn 9541 # 18) D, prosome, dorsal; E, prosome, lateral – both with gut visible through body wall. Swollen specimen. (♀ T.L. 4·5mm, Stn 9541 # 22) F, gut, dorsal; G, gut, lateral. Scales 1mm.

## Vertical distribution

### *Benthomisophria palliata*

The vertical distributions of the copepodid and adult stages of *B. palliata* caught in the RMT 1 series at Station 9541 are shown in Figure 17. The two hauls that fished between 5–20m off the bottom ( # 18 and 19, Table 1) have been combined, and as there was no sexual difference in distribution the adults have also been combined. *B. palliata* is too small to be adequately sampled by the RMT 8 and the Copepodid I and II stages, with mean body lengths of 0·79 and 1·03mm respectively, are probably not taken effectively by the RMT 1 either. The results from the RMT 1 series at Station 9131 are similar to those for Station 9541 but this series was incomplete. The numbers of specimens in each haul have been corrected for an equal volume of water filtered.

The depth range of all stages is very wide, extending from 2500m to the bottom. In addition, a single adult was caught between 2000 and 2500m. There are no apparent differences in depth distribution between the various stages or between the sexes. At no depth is the species abundant, but there is a general increase in numbers in the deepest samples taken within 500m of the bottom. After correction for the volume of water filtered, the greatest number of specimens caught in a single haul (all stages combined) was 136, in the 5–20m off the bottom sample. Assuming an even distribution this represents 1 animal per $106m^3$ of water. The largest number of any particular stage caught was 45 adults, also in the 5–20m sample. This represents 1 animal per 322m³. In terms of biomass these figures are infinitesimal.

The mean body length at each depth of each stage of *B. palliata* was calculated, using the same RMT 1 series of hauls from Station 9541 (Fig. 18). The mean length of each copepodid stage is more or less uniform throughout the depth range. Both males and females, however, are apparently larger in the samples taken within 500m of the bottom.

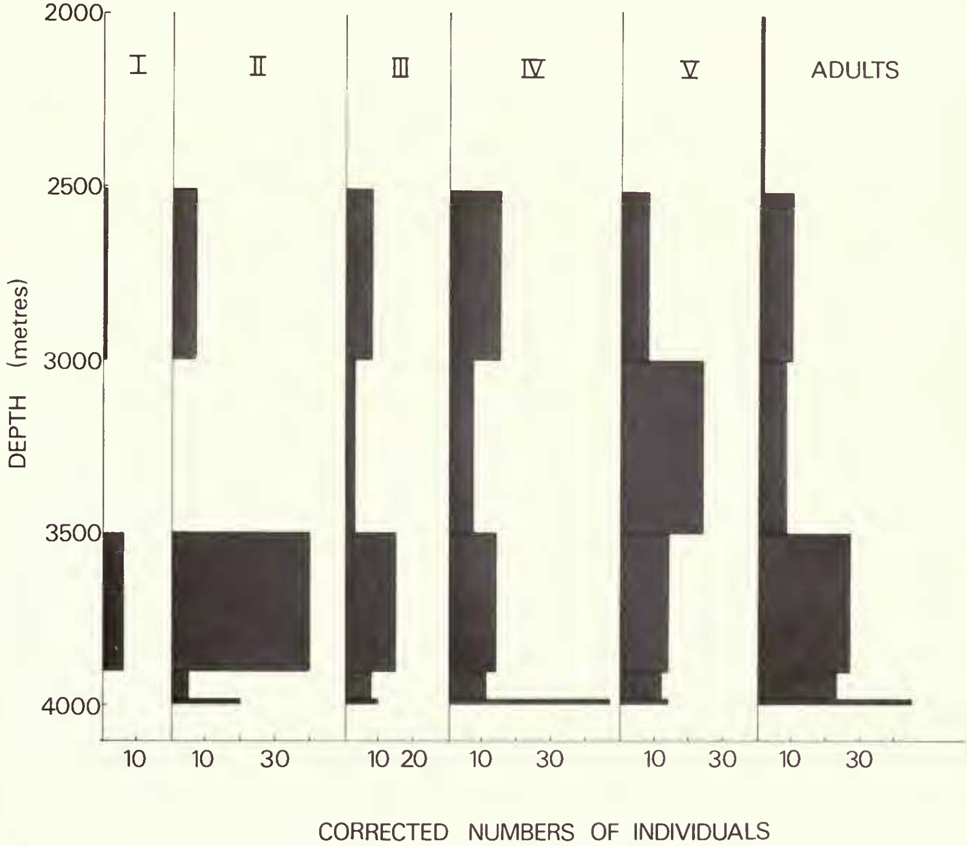


**Fig. 17** Vertical distributions of the Copepodid and adult stages of *B. palliata*, based on RMT 1 series at Station 9541.

Some stages (Co. V, ♂ and ♀) show distinct large and small size morphs (page 33). In Co. V stage both small and large morphs occur throughout the depth range. In the adults small morphs are found at all depths but large ones are not. Females longer than 3·67mm and males longer than 3·45mm in total body length were found only in the deepest hauls taken within 500m. of the bottom. It is, therefore, only this deep population that shows the total range in body length and the bimodal size frequency distribution (Figs 14 & 15).

### *Benthomisophria cornuta*

The numbers of *B. cornuta* caught in each haul are shown in Table 3. These numbers are insufficient to permit detailed analysis and it is likely that the RMT 1 does not effectively sample the copepodid stages of this small species.

The catch data suggest that, as with *B. palliata*, the vertical range occupied by this species is very wide, extending from 2500m to the bottom.

## Phylogenetic relationships

The order Misophrioida comprises two genera, *Misophria* and *Benthomisophria,* and three species *M. pallida, B. palliata* and *B. cornuta.* The species and genera are most clearly separated on the basis of the segmentation of the leg 5. In *Misophria pallida* the leg 5 consists of 3 distinct segments. In *Benthomisophria palliata* the leg 5 is 2-segmented. The basal segment is notched laterally and bears a small suture line indicating that it probably represents two incompletely fused segments, derived from the 3-segmented type of leg 5 found in *M. pallida.* In *B. cornuta* the process of fusion of the segments has progressed further and the leg 5 is 1-segmented in the adult. The condition found in the Copepodid IV stage of this species (Fig. 8L) suggests that the single segment is derived from the fusion of two distinct segments.

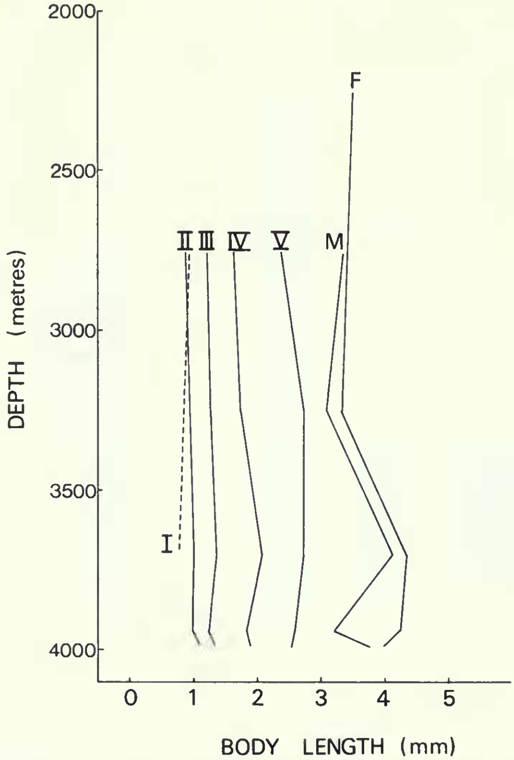


**Fig. 18** Mean body length, at each depth, of the Copepodid stages and the adult male (M) and female (F) of *B. palliata.* (Copepodid I line is hatched). Based on data from RMT 1 series at Station 9541.

There appears to be a phylogenetic transformation series from the plesiotypic 3-segmented condition, via the intermediate 2-segmented condition, to the apotypic 1-segmented condition. The cladogram (Fig. 19) shows the probable phylogenetic relationships between the 3 species included in the Misophrioida.

Hulsemann & Grice (1964) reviewed the historical aspects of the classification of the Family Misophriidae within the Copepoda. *Misophria* has long been recognized as representing a distinct group within the Copepoda. Giesbrecht (1892) placed *Misophria* in a separate family, the Misophriidae and, according to Gurney (1927), Giesbrecht's families are now largely regarded as equivalent to orders. Gurney (1933) proposed that *Misophria* should be regarded as the type of a separate order, the Misophrioida. Lang (1948) erected the suborder Propodoplea, to contain the family Misophriidae. In a recent work on the classification of the Copepoda, Kabata (1979) regarded the Misophrioida as an early offshoot from the podoplean line and this system has been adopted in the present account.

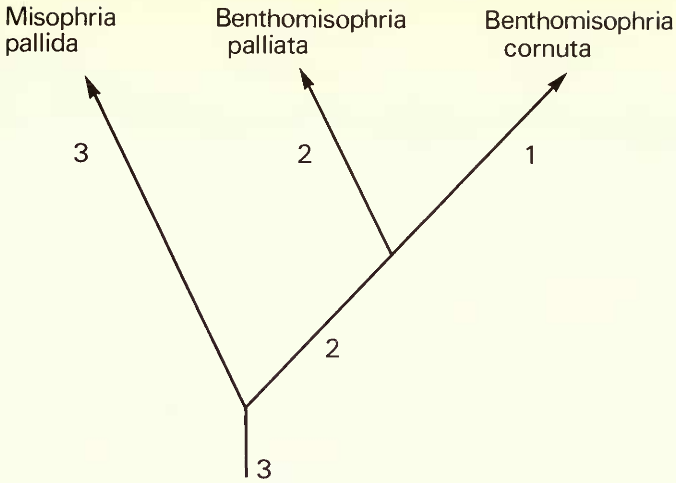


**Fig. 19** Cladogram showing the probable phylogenetic relationships between the three species comprising the Misophrioida. (1,2 or 3 denotes the number of segments in the adult leg 5).

## Discussion

The samples analysed are the first to have been taken close to the bottom in the total water column programme initiated by the Institue of Oceanographic Sciences in 1976. The new near-bottom sampling technique employs bottom indicator switches that are rather inaccurate and difficult to use. A near bottom echo sounder is being developed to facilitate this type of sampling.

*B. palliata* has rarely been caught but it has a wide geographical distribution. It was recorded by Sars (1909) from 3 stations in the northeastern Atlantic in hauls made with open nets fished from depths of 2585 (also given as 5285m), 1414 and 3465m. Tanaka (1966) found a single specimen of each sex between 1000–0m depth in the Pacific adjacent to the Izu region of Japan. The present material extends its geographical range southwards in the eastern North Atlantic.

*B. palliata* has not previously been caught with closing nets. The new data indicate that *B. palliata* is bathypelagic but that its vertical distributions show little affinity with the sea bottom. It occupies a wide depth range and has no well defined optimum depth. Sars' (1909) specimens were presumably caught in the deep parts of his tows and Tanaka's (1966) record is the shallowest of this species.

Only two specimens of *B. cornuta* have been recorded, both female. One was taken in the northeastern Atlantic at 40°03·5′N 19°57′W, between 4750 and 4000m depth (Hulsemann & Grice, 1964), and the other off Izu, Japan between 1000–0m (Tanaka, 1966 – as *M. maculata*). The present record extends the known geographical of *B. cornuta* southwards in the North Atlantic. Too few specimens were taken to clarify its vertical distribution but it seems similar to that of *B. palliata,* with a wide depth range.

The analysis of body length frequency distribution in *B. palliata* indicated that two size morphs of *B. palliata* were present in the population. There was a slight difference in the vertical distribution of the two morphs in the adults of both sexes but there were no other morphological differences. This kind of size dimorphism has been observed in several other planktonic copepods, such as *Oncaea venusta* Philippi, 1843 (Boxshall, 1977). The explanation of this dimorphism must await additional seasonal, geographical and ecological data.

The ability to gorge and distend the body wall when the opportunity arises has now been found in three distinct crustacean groups, as well as in several midwater fish (Murray & Hjort, 1912). In *Benthomisophria* and the amphipod *Paralicella* Chevreux, 1908 the gut is very elastic but has no other obvious structural modification. *Nebaliopsis typica* G. O. Sars, 1887 is specialized in having a very distensible mid gut sac (Rowett, 1943). When this is filled the cephalothorax is so distended that its posterior region protrudes behind the carapace (Cannon, 1931 & 1946). *N. typica* is bathypelagic and is believed to feed by sucking eggs. The mid gut sac is presumed to be a storage organ enabling the animal to take maximum advantage of an irregular food supply (Rowett, 1943; Cannon, 1946). Except for the amphipods all the animals that are known to have the ability to gorge live in midwater at depths where food items are likely to be scarce. It is perhaps to be expected that modifications to enable opportunistic feeding exist in such an environment. Bottom living animals possibly have a more continuous supply of food available to them, both from the benthic community and from the 'rain' of debris. The ability to utilize infrequent large particles of food is, however, clearly advantageous and *Paralicella* is adapted accordingly.

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## References

**Baker, A. de C., M. R. Clarke & M. J. Harris.** 1973. The N.I.O. combination net (RMT 1 + 8) and further developments of rectangular midwater trawls. *J. mar. biol. Ass. U.K.* **53** : 167–184.

**Boeck, A.** 1864. Oversigt over de ved Norgs Kyster iagttagne Copepoder henhøvende tie Calanidernes, Cyclopidernes og Harpacticidernes Familiar. *Forh. VidenskSelsk. Krist.* **1864** : 226–281.

**Boxshall, G. A.** 1977. The planktonic copepods of the northeastern Atlantic Ocean: some taxonomic observations on the Oncaeidae (Cyclopoida). *Bull. Br. Mus. nat. Hist.* (Zool.) **31** : 103–155.

**Brewer, P. G., D. W. Spencer, P. G. Biscaye, A. Hanley, P. L. Sachs, C. L. Smith, S. Radar & J. Fredericks.** 1976. The distribution of particulate matter in the Atlantic Ocean. *Earth planet. Sci. Lett.* **32** : 393–402.

**Cannon, H. G.** 1931. Nebaliacea. *'Discovery' Rep.* **3** : 199–222.

—— 1946. *Nebaliopsis typica. 'Discovery' Rep.* **23** : 213–222.

**Dudley, P. L.** (1966). *Development and Systematics of some Pacific marine symbiotic copepods.* Univ. Washington Press: Seattle & London. 282 pp.

**Giesbrecht, W.** 1892. Systematik und Faunistik der pelagischen Copepoden des Golfes von Neapel und der angrenzenden Meeresabschnitte. *Fauna Flora Golfo Napoli.* **19** : 1–831.

**Gurney, R.** 1927. Zoological results of the Cambridge Expedition to the Suez Canal, 1924. XXXIII. Report on the Crustacea:– Copepoda (Littoral and Semi-parasitic). *Trans. zool. Soc. Lond.* **22** : 451–577.

—— 1933. Notes on some Copepoda from Plymouth. *J. mar. biol. Ass. U.K.* **19** : 229–304.

**Hulsemann, K. & Grice, G. D.** 1964. A new bathypelagic species of *Benthomisophria* (Copepoda: Misophriidae) from the North Atlantic. *Zool. Anz.* **173** : 259–264.

**Kabata, Z.** 1979. *Parasitic Copepoda of British Fishes.* Ray Society: London. 459 pp.

**Katona, S. K.** 1973. Evidence for sex pheromones in planktonic copepods. *Limnol. Oceanogr.* **18** : 574–583.

**Lang, K.** 1948. Copepoda 'Notodelphyoida' from the Swedish West Coast with an outline on the systematics of the copepods. *Arkiv. Zool.* **40A** (14) : 1–36.

**Murray, J. & Hjort, J.** 1912. *The Depths of the Ocean.* Macmillan & Co. Ltd.: London. 821 pp.

**Roe, H. S. J. & Harris, M. J.** in press. A new accoustically telemetering deep sea photometer with some observations on underwater light in the North East Atlantic. *Deep-Sea Res.*

**Rowett, H. G. Q.** 1943. The gut of Nebaliacea. *'Discovery' Rep.* **23** : 1–17.

**Sars, G. O.** 1903. *An account of the Crustacea of Norway. V. Copepoda Harpacticoida.* Bergen Museum. Pts. I–II : 1–28.

—— 1909. Note préliminaire sur trois formes rémarquables de copépodes provenant des Campagnes de S.A.S. Le Prince Albert de Monaco. *Bull. Inst. Océanogr. Monaco.* **147** : 1–8.

**Shulenberger, E. & Barnard, J. L.** 1976. Amphipods from an abyssal trap set in the north Pacific gyre. *Crustaceana.* **31** : 241–258.

**Steedman, H. F.** 1974. Laboratory methods in the study of marine zooplankton. *J. Cons. perm. int. Explor. Mer.* **35** : 351–358.

**Tanaka, O.** 1966. Some rare species of Harpacticoida from the Izu region. *Mar. biol. Ass. India. symposium ser. 2. Proc. Symp. on Crustacea.* **1** : 51–56.

**Thurston, M. H.** 1979. Scavenging abyssal amphipods from the North-East Atlantic Ocean. *Mar. Biol. Berlin.* **51** : 55–68.

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